SUMMER 2005 VOL. 56, No. 2

VIRGINIA JOURNAL OF SCIENCE

OFFICIAL PUBLICATION OF THE VIRGINIA ACADEMY OF SCIENCE

THE VIRGINIA JOURNAL OF SCIENCE

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VIRGINIA JOURNAL OF SCIENCE
OFFICIAL PUBLICATION OF THE VIRGINIA ACADEMY OF SCIENCE

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Virginia Journal of Science
Volume 56, Number 2
Summer 2005

Phytoplankton Development Within Tidal Freshwater Regions of Two Virginia Rivers, U.S.A.

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ABSTRACT

Phytoplankton composition and the range of seasonal patterns of abundance are presented for the tidal freshwater regions in two Virginia rivers based on data accumulated monthly from 1986 through 1999. Diatoms dominated the flora during spring, summer, and fall, whereas, other taxonomic categories were more representative when the river flow rates decreased, allowing for a more stable water system and increased residency time within this tidal region during summer and early fall. This summer/fall period was associated with increased water temperatures, higher productivity rates and chlorophyll levels, increased total phytoplankton abundance and species diversity. The major components of the summer flora were autotrophic picoplankton, chlorophytes, and cyanobacteria. Mean, maximum, and minimum monthly abundance figures are given for the different phytoplankton categories, and total phytoplankton biomass and abundance, over this 13-year period. Although one station showed considerable influx of oligohaline water into its tidal freshwater region during sampling, no significant relationships were associated with phytoplankton biomass or productivity to these changing salinities.

Key words: Phytoplankton, Virginia, Rappahannock, Pamunkey, tidal freshwater

INTRODUCTION

Marshall and Burchardt, 1998, have described the tidal freshwater region as a unique component of a river system. It is daily influenced by tidal action, yet, the location of this region in a river will move upstream or downstream, depending upon daily or seasonal changes in the occurrence and duration of rainfall, or due to various hydrodynamic events that would influence tidal amplification and flow within the river. The tidal freshwater is defined as the region within a river possessing daily tidal movements bordered upstream by freshwater (<0.5 ppt) lacking a tidal response, and downstream by tidal waters of greater salinity. This is the tidal oligohaline region that is characterized by salinities 0.5 to 5.0 ppt. The algae entering the tidal fresh region upstream are dominated by chlorophytes, diatoms, and cyanobacteria in contrast to downstream flora (e.g. in oligohaline and mesohaline regions) where estuarine diatoms and dinoflagellates are the dominant taxa (Haertel et al., 1969; Forester, 1973; Jackson et al,, 1987; Marshall and Alden, 1990). The tidal freshwater region may also contain a small percentage of estuarine species. These are introduced from sub-pycnocline waters advancing upstream during periods of low river discharge and when tidal

movement advances farther upstream into normally tidal freshwater regions (Marshall and Burchardt, 1998). Farrell, 1994 and Schmidt, 1994, have associated increased diatom abundance with increased river discharge common during spring months. Marshall and Burchardt ,1998, reported peak diatom development occurred in the tidal freshwater James River (Virginia) during periods of increased river discharge, with chlorophytes, cyanobacteria, autotrophic picoplankton, and euglenophytes having greater abundance during summer and periods of more stable water conditions. This study reports on the phytoplankton populations and water quality of tidal freshwater stations in the Pamunkey River and Rappahannock River, both located in southeast Virginia, U.S.A.

The Rappahannock River (ca. 341 km in length) is a major tributary of the Chesapeake Bay located in the eastern coastal plain of Virginia. The river flows southeasterly through predominantly forest, crop-land, and pasture before entering Chesapeake Bay. The Pamunkey River (ca. 96 km long), is also located in Virginia, just south of the Rappahannock River, flowing southeasterly through mostly forest and land used in agriculture, or for raising live stock. The river terminates at its confluence with the Mattoponi River, forming the York River that continues parallel to the Rappahannock River before entering the Chesapeake Bay. The climate in this region is moderate with an average annual temperature ca. 14^{o}C and average rainfall ca. 106-116 cm.

Previous phytoplankton studies in the Pamunkey/York and Rappahannock rivers include those by Marshall and Alden, 1990; Marshall and Affronti, 1992; Marshall and Nesius, 1993; and Marshall and Burchardt, 2004. Their results identify the characteristic species composition and abundance in these rivers. Spring, summer, and fall productivity and abundance maxima were described in relation to dominant flora, with the autotrophic picoplankters being a major component and contributor to productivity during summer (Marshall and Nesius, 1993). Downstream studies in the York River section are mainly in the lower reach of the river where summer dinoflagellate blooms are common (Mackiernan, 1968; Zubkoff et al., 1979). Relationships of phytoplankton distribution and stratification to tidal cycles in the York River are discussed by Haas et al., 1981 and Ducklow, 1982.

The objectives of this study are to identify the seasonal developmental patterns of the phytoplankton composition within the tidal freshwater regions of two rivers. Using a long-term data base the annual biomass patterns are described to indicate the range of population fluctuation that may occur within these systems. Additional characteristics and environmental relationships between the phytoplankton community and several physical and chemical factors associated with these rivers are also presented.

METHODS

Monthly water samples were taken at the tidal freshwater stations in the Rappahannock River (TF3.3, 38^{o} 01' 07" N; 76^{o} 54' 30"W) and the Pamunkey River (TF4.2, 37^{o} 34' 47"N; 77^{o} 01' 19"W) from July 1986 through December 1999 (13.5 years) (Figure1.). The mean depths at these stations were ca.6.8 m and ca.8.9 m respectively for TF3.3 and TF4.2. At each station a vertical series of five 3 liter water samples were taken from the upper third of the water column and placed in a carboy, mixed, and a 500 mL sample drawn off and fixed with Lugol's solution. These samples were analyzed using a modified Utermöhl technique following a series of settling and

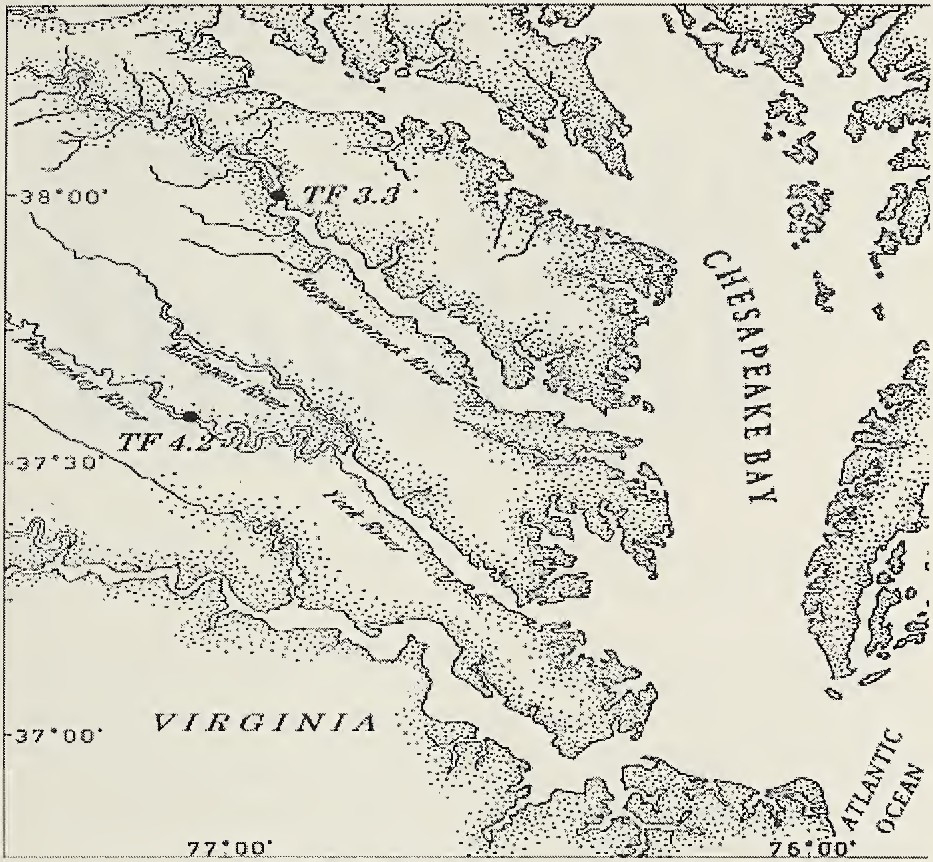

FIGURE 1. Sampling stations: Station TF3.3 (38° 01' 07" N; 76° 54' 30" W) located in the Rappahannock River and Station TF4.2 (37° 34' 47"N; 77° 01' 19" W) in the Pamunkey River, Virginia.

siphoning steps over time to produce ca. 40 mL concentrate of the original sample for subsequent microscopic analysis (Marshall and Alden, 1990). Identification and cell abundance for each sample were based on a minimum microscope cell count of 200, using a minimum of 10 random fields examined at 315X and 500X, plus including other species observed by scanning the entire counting chamber at 125X. An additional 24 samples from 1998-1999 at these stations were examined for further species identification. The autotrophic picoplankton cells were identified using epifluorescence microscopy as described in Marshall, 1995. Also determined were ^{14}C productivity rates, beginning in July 1989, using protocols described by Marshall and Nesius, 1993. Biomass was determined from cell volume measurements made for the different species and transferred to cell carbon according to Smayda, 1978. The Margalef Diversity Index was used regarding species diversity. River water discharge rates were provided by the U.S. Geological Survey from locations near station TF3.3 (38°19'20" N, 77°31'05"W), and station TF4.2 (37°46'03"N, 77°19'57"W). Surface water temperatures and Secchi readings were taken on station during each sampling period. Additional water quality data from these stations were provided by the Virginia

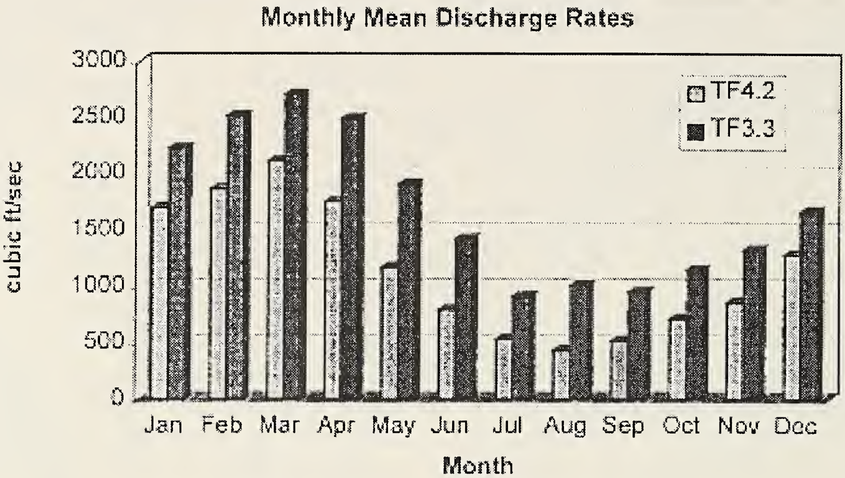

FIGURE 2. Monthly mean discharge rates (1986-1999) for stations adjacent to stations TF3.3 in the Rappahannock River and TF4.2 in the Pamunkey River

Chesapeake Bay Monitoring Program. These included analysis of water taken on station for total nitrogen (TN), total phosphorus (TP), total suspended solids (TSS), and dissolved oxygen. Seasonal references are defined as winter including the months of December, January, and February, followed by the sequential 3-month periods for spring, summer, and fall. A Student T-test was used to determine distribution relationships of the phytoplankton and productivity to salinity differences noted during the sampling period at the Rappahannock River station TF3.3.

RESULTS

The drainage area above the two sampling stations is 4,133 km^2 and 1,739 km^2 for the Rappahannock and Pamunkey Rivers respectively, with the monthly discharge pattern similar at both sites. Peak water flow at these stations was from winter through early summer (December-June), with decreased flow in mid-summer that continued into early fall (July-September), after which flow increased, from mid-fall into the winter months (Figure 2). The summer minimum and winter-spring maximum of the mean monthly rates of flow differed at the two stations, ranging from 25.8 $m^3\ sec^{-1}$ (912 $ft^3\ sec^{-1}$) in July to 76.7 $m^3\ sec^{-1}$ (2,711 $ft^3\ sec^{-1}$) in March for the Rappahannock River, and from 12.4 $m^3\ sec^{-1}$ (438 $ft^3\ sec^{-1}$) in August to 52.7 $m^3\ sec^{-1}$ (1,863 $ft^3\ sec^{-1}$) in February in the Pamunkey River. The major annual influence to these seasonal flow patterns was the amount of rainfall within these two river watersheds. U.S. Geological Survey records of flow rates began in 1951 and are the basis for estimating average and extreme periods of monthly and annual mean flow. Those annual rates that were within the 25 to 75 percentile of this data set were considered average, or normal. If the annual rate falls below the 25 percentile it would be considered a "dry" year, whereas, flow rates above the 75 percentile would be classified as "wet" years. During the 13 years of this study, the annual flow into these rivers varied greatly. There were 5 "wet" and 5 "dry" years, and 3 years where the flow may be considered "normal",

or "average". As these differences in annual rainfall occur, they will have major influence on the horizontal range and dynamics associated with the tidal fresh and various downstream salinity regions of these rivers. Progressing into this study it became evident that salt-water intrusion frequently occurred at TF3.3 in the Rapppahannock River. Over the 13 year period, Station TF3.3 had freshwater status (<0.5 ppt) 40.6% of the collection dates, whereas, during 59.4% of the dates the salinity was >0.5 ppt. Tidal freshwater status was associated with periods of increased rainfall and coincided with the spring diatom bloom (e.g. January-May). Periods when salinity intrusion into this area was most common occurred during the summer and fall months (June-October). In contrast, station TF4.2 in the Pamunkey River had freshwater status on 97.7% of the collection dates. Overall, more water flowed through the Rappahannock station, and at a faster rate, than at the Pamunkey station.

Both stations had similar surface water temperature patterns reaching highs of ca. 28 ^{o}C in July, with lowest mean monthly temperatures occurring in February at TF3.3 (3.6 ^{o}C) and in January at TF4.2 (4.8 ^{o}C). The dissolved oxygen concentrations were inversely related to the water temperature with lowest values during summer and highest in winter. The mean monthly range was from 6.5 in July to 12.2 mg L^{-1} at TF3.3 in February, and 4.7 in August to 11.8 mg L^{-1} in February at TF4.2. Monthly periods of peak total suspended solids (TSS) varied, with greatest loads during periods of high flow in spring (Figure 3). At station TF3.3, TSS were consistently higher than at TF4.2, ranging from 20.6 mg L^{-1} in late summer (August) to 51.2 mg L^{-1}, in late winter (February). The TSS at station TF4.2 ranged from monthly means of 13.5 (Sept.) to 18.9 mg L^{-1} (Dec.), showing a rather stable pattern throughout the seasons. The TSS increased gradually from summer into fall, reaching highest concentrations from early winter through spring. Maximum records of 140 and 168 mg L^{-1} at TF3.3 occurred in January and May respectively. Mean monthly Secchi readings ranged from 0.31 m (February-April) to 0.64 m (September) at TF3.3, and from 0.51 m (January) to 0.82 m (September) at TF4.2. The annual monthly means for TF3.3 and TF4.2 were 0.45 m and 0.70 m respectively. These results indicated an association between increased water flow to higher TSS concentrations and reduced Secchi readings at TF3.3, in contrast to the reverse relationships during periods of reduced flow during summer. However, this relationship was less clear at TF4.2, where a lower and more consistent presence of TSS was recorded. More suspended solids were carried in the Rappahannock, with the mean and range of Secchi readings less than in the Pamunkey River.

There were differences in the total nitrogen (TN) patterns at the two stations (Figure 3). At TF3.3, peak levels (monthly means) occurred in early spring (1.32 mg L^{-1}, March), decreasing into the summer and fall months to a low of 0.73 mg L^{-1} (August) to increase through late fall and winter to the spring highs. Maximum levels occurred from mid-winter through mid-spring. The mean range at TF4.2 showed less variability, increasing from 0.69 mg L^{-1} (November) to 0.88 mg L^{-1} (June), resulting in the mean total nitrogen being higher at TF3.3 than at TF4.2. The mean monthly total phosphorus (TP) at TF3.3 ranged between 0.06 and 0.12 mg L^{-1} throughout the seasons, showing a decrease from late spring into summer, before rising again in winter (Figure 3). At TF4.2, the monthly means ranged from 0.06 mg L^{-1} in the fall (October), to a spring (March) high of 0.12 mg L^{-1}. Maximum TP occurred during winter-spring at TF3.3 and in summer at TF4.2 (Figure 3). Both stations had pulses that occurred in early spring, mid-summer, and fall, with the highest monthly means at TF3.3. The mean

TN:TP ratio ranged from 7.6 to 12.6 at TF3.3, and 8.2 to 13.8 at TF4.2, with the lowest ratios occurring May through July at TF3.3, and in July and August at TF4.2. Thus, there were general differences in the periods of maximum levels of nitrogen and phosphorus in these rivers. In the Rappahannock, the greatest TN concentrations occurred in spring and the lowest in late summer, corresponding to the high and low flow periods in this river. In the Pamunkey, the highest TN concentrations were in early summer, and least in late fall. TP maxima occurred in winter and summer respectively for the Rappahannock and Pamunkey. In the Pamunkey, this summer TP high coincided with high productivity, decreased river flow, and increased concentrations of cyanobacteria, picoplankton, and other algae.

Chlorophyll *a* increased into summer from a winter low, with concentrations greater at TF3.3 than at TF4.2 (Figure 4). At TF3.3, the monthly mean ranged from 2.9μg L^{-1} (January) to 13.9 μg L^{-1} (August). There was generally a late spring (May) development, a slight decrease in early summer, then highs from mid-summer through fall. At TF4.2, there was chlorophyll a increase during summer, with peaks in July and August (9.27, 8.37 μg L^{-1}), to a January low (2.09 μg L^{-1}). Also present were periods of maximum chlorophyll a concentrations from spring through fall at both stations. The mean productivity rates for both stations were lowest during mid-winter, then gradually increased to peaks during late spring, summer, and early fall, before declining into winter (Figure 5). The higher rates were consistently recorded at station TF3.3 and ranged from 12.2 mg cm^3 h^{-1} (Dec.) to 156.9 mg c m^3 h^{-1} (May). Increased productivity extended from April through August. At TF4.2, productivity ranged from 5.2 mg cm^3 h^{-1} (Dec.) to highs of 43.1 and 46.3 mgcm^3 h^{-1}, for July and August respectively. This pattern was similar to seasonal chlorophyll a concentration differences between the two river stations with highest mean rates of productivity during the summer months.

A total of 268 phytoplankton taxa were identified at these two stations (Marshall and Burchardt, 2004). There were 208 and 232 phytoplankton taxa represented at the Rappahannock River and Pamunkey stations respectively. Sixty one percent of the taxa were present at both stations, with the general composition of the dominant species similar. The major difference in composition was the estuarine taxa at the Rappahannock station during periods (summer/early fall) of increased salinity and upstream advancement of tidal water from the oligohaline region. Collectively for both stations, there were 133 Bacillariophyceae, 63 Chlorophyceae, 31 Cyanobacteria (cyanoprokaryotes), 10 Dinophyceae, 11 Euglenophyceae, 6 Xanthophyceae, 5 Cryptophyceae, and 9 Chrysophyceae. The autotrophic picoplankton was identified as a separate and composite group from the above categories and consisted predominantly of single celled cyanobacteria. Figures 6 and 7 show the monthly maximum and minimum records, and means for the major phylogenetic categories. The two extremes indicated the past ranges recorded for these categories. Variability also occurred over this time period in taxon representation in each water sample analyzed, with maximum representation of taxa per water sample in the summer months and least in winter (e.g. at TF3.3 these totals were 73 and 26 taxa; and at TF4.2, 59 and 22 taxa). The Margalef Diversity Index maxima during this period ranged from 2.3 (January) to 4.0 (July) at TF4.2, with the mean monthly range from 1.6 (March) to 2.4 (August). The diversity maxima at TF3.3 ranged from 2.3 (January) to 4.0 (July), with monthly means from 1.6 (March) to 2.4 (August). Diversity was lowest at both stations in late winter/early

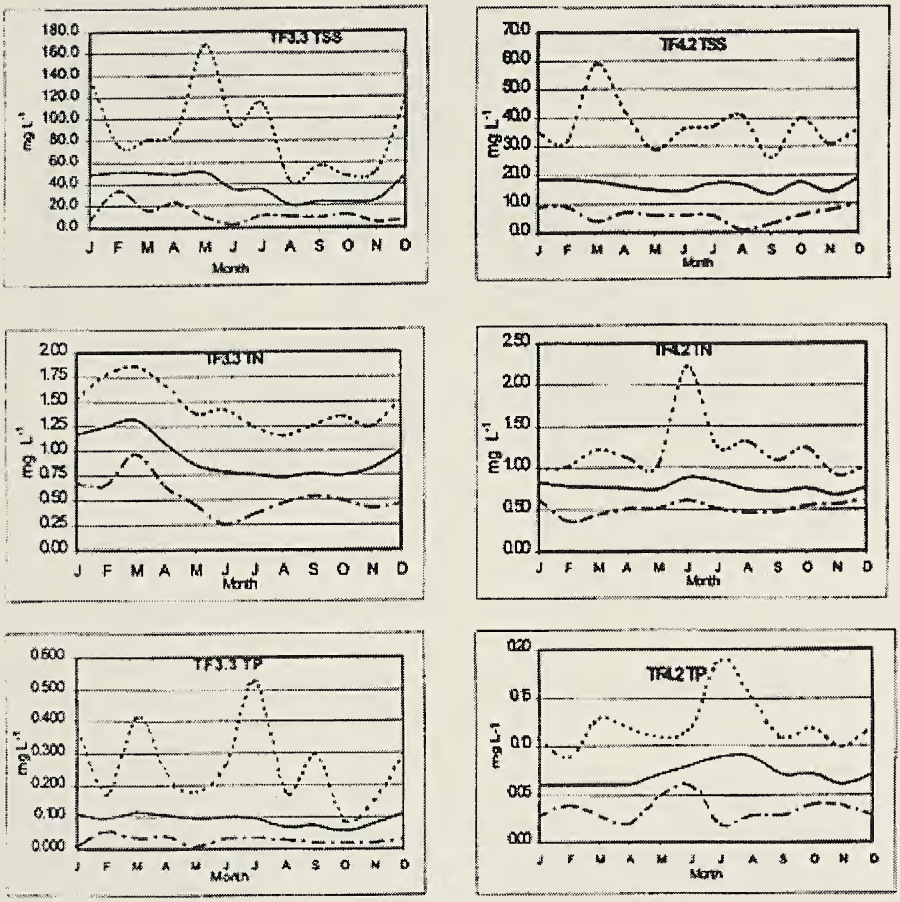

FIGURE. 3 Monthly concentrations for chlorophyll *a*, total phytoplankton abundance, and total phytoplankton biomass at TF3.3 and TF4.2, 1986-1999, indicating mean (solid line), maximum (dotted line), and minimum (dot-dash line) records.

spring when flow in the rivers was greatest, increasing into summer during periods of reduced flow rates.

In presenting total phytoplankton abundance and total phytoplankton biomass, the mean monthly values, plus the cell maxima/minima amounts are indicated (Figure 4). The seasonal patterns of phytoplankton development show seasonal abundance peaks in mid-winter, spring, mid-summer and fall (Figure 4). The abundance figures do not include the picoplankton, however, the picoplankton biomass was included in the total phytoplankton biomass. The mean monthly range at TF3.3 was 6.8 x 10^6 cells L^{-1} (February) to 35.5 x 10^6 cells L^{-1} (July), with the highest cell concentrations as 108.8 x 10^6 cells L^{-1} (July). At TF4.2, abundance ranged from 24.0 x 10^6 cells L^{-1} (March) to 12.8 x 10^6 cells L^{-1} (July), with the maximum of 35.9 x 10^6 cells L^{-1} (January). The phytoplankton biomass mimics these patterns, but with greater biomass during spring and fall, followed by winter and summer at TF3.3. In contrast, at TF4.2 the summer biomass was greater than in the other seasons. At TF3.3 the phytoplankton biomass

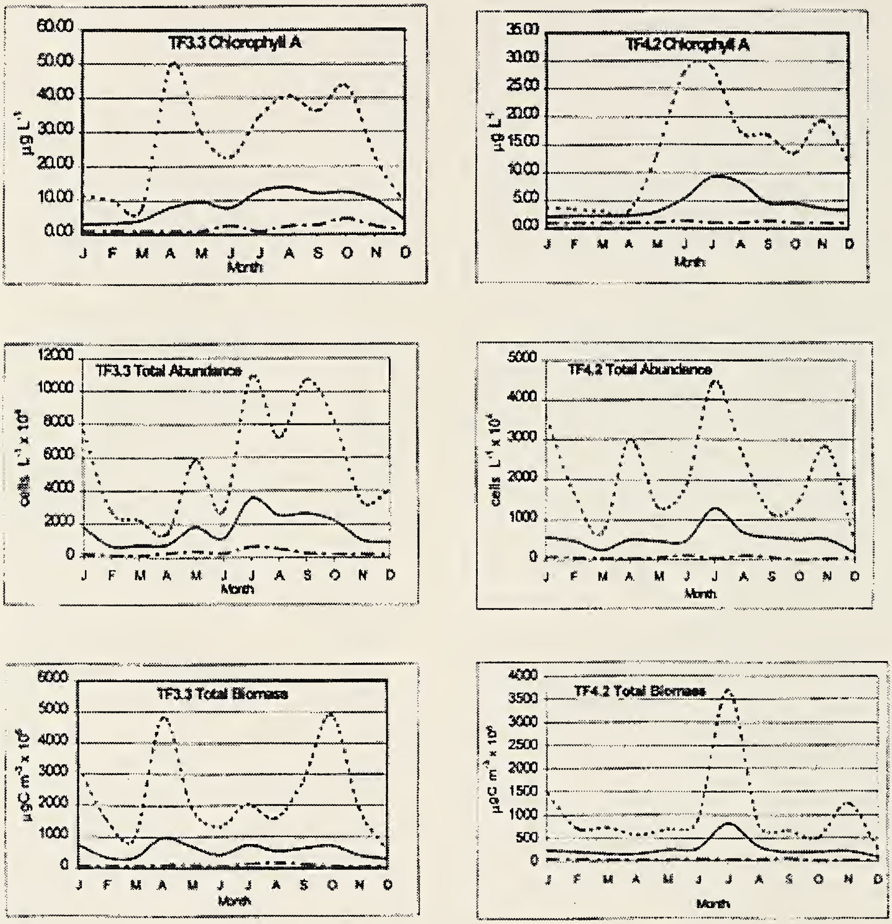

FIGURE 4. Monthly concentrations of chlorophyll *a*, total phytoplankton abundance, and total phytoplankton biomass at TF3.3 and TF4.2, 1986-1999, indicating mean (solid line), maximum (dottedline), and minimum (dot-dash line) records.

ranged from 279 to 979 x 10^6 μgcm^3 (December, April), with the maximum of 4,902 x 10^6 μgCm^3 (October), and the least as 48 μgcm^3 (November). Biomass peak records were associated with the diatoms. At TF4.2, the biomass ranged from 91 to 818 x 10^6 μgcm^3 (December, July), with a maximum record of 3,694 10^6 μgcm^3 in July. Since there were frequent salinity differences occurring in the tidal freshwater station (TF3.3) in the Rappahannock River, student T-tests were run to determine the degree of phytoplankton/salinity relationships present. The results indicated there were no significant differences between total phytoplankton biomass ($p = 0.296$), diatom biomass ($p = 0.116$), cyanobacteria biomass ($p = 0.399$), or productivity ($p = 0.823$), to salinity values <0.5 and those >0.5 ppt. at this location.

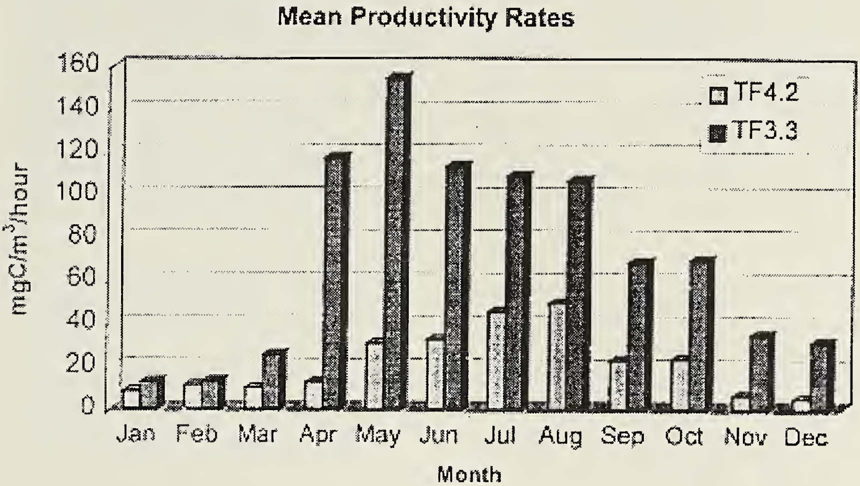

FIGURE 5. Mean monthly carbon productivity rates for stations TF3.3 and TF4.2 from July 1989 to December1999.

1. Bacillariophyceae:

The diatoms had mean monthly concentration peaks occurring during winter/spring, summer, and fall at both stations, with greater abundance recorded in the Rappahannock River (Figure 6). Diatoms represented the seasonally dominant flora at both stations. Mean monthly minimum and maximum concentrations were 3.2 to 11.4 x 10^6 cells L^{-1} (December, May) at TF3.3, and 1.0 to 3.5 x 10^6 cells L^{-1} (December, July) at TF4.2. The recorded minimum and maximum concentrations over this period were 0.5 and 53.1 x 10^6 cells L^{-1} at TF3.3 (October, January), and 0.007 to 28.2 x 10^6 cells L^{-1} at TF4.2 (October, April). The diatoms had a diverse assemblage of taxa that included the major producer of the spring diatom pulse, *Skeletonema potamos*, and an abundance of planktonic centrics and benthic pennates. Most common were *Asterionella formosa, Aulacoseira granulata, A. granulata v. angustissima, A. distans, A. varians, Cyclotella Meneghiniana, C. striata, Navicula crytocephala, N. radiosa, Nitzschia acicularis, Surirella ovata*, and a variety of other pennates and centrics <20 microns in size. This composition and dominant freshwater taxa were similar in both rivers. However, the summer/fall flora at TF3.3 contained ample representations of estuarine species, specifically *Skeletonema costatum*. The mean abundance for the diatoms was moderate within their maximum and minimum concentrations. However, there existed considerable fluctuation in the year-to-year patterns that were influenced by flow through the system and the initiation time for diatom development to occur. The maxima depicted here also illustrates the range of the potential growth for this community. The historic maxima during spring, summer, and fall that occurred at both stations greatly exceeded the mean concentrations.

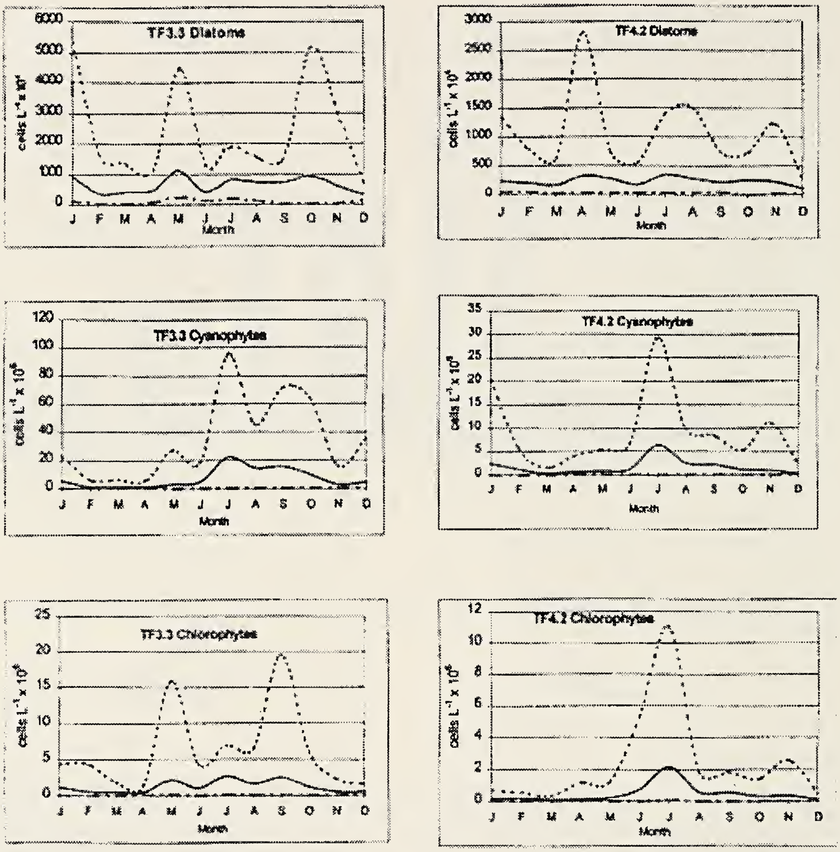

FIGURE 6. Monthly concentrations for diatoms, cyanobacteria, and chlorophytes at stations TF3.3 and TF4.2, 1986-1999, indicating mean (solid line), maximum (dotted line), and minimum (dot-dash line) records.

2. Cyanobacteria:

At both stations, the predominant development of the cyanobacteria (cyanoprokaryotes) occurred from mid-summer into mid-fall, then decreased in late fall and winter (Figure 6). However, there were sporadic seasonal highs throughout the year with the mean monthly range from 1.2 to 22.2 x 10^6 cells L^{-1} (April, July) at TF 3.3, and at TF4.2, from 0.2 to 6.3 x 10^6 cells L^{-1} (December, July). Maxima at the two stations were 95.5 and 29.2 x 10^6 cells L^{-1} respectively for TF3.3 and TF4.2, with both occurring in July. Several filamentous taxa were common during winter and early spring. These included *Oscillatoria limnetica, O. granulata, O. irregua, O. pseudominima, Nodularia spumigena f. litorea*, and *Lyngbya contorta*. Noted throughout the year was *Dactylococcopsis rhapidioides*. This species, plus *D. rhapidioides v. falciformis, O. granulata, O. angustissima, Microcystis aeruginosa, M. incerta,* and *Merismopedia marssonii* were common representatives of the summer/early fall flora. The same tidal freshwater species occurred at both stations, with previous records of their abundance common in downstream oligohaline and mesohaline regions of these

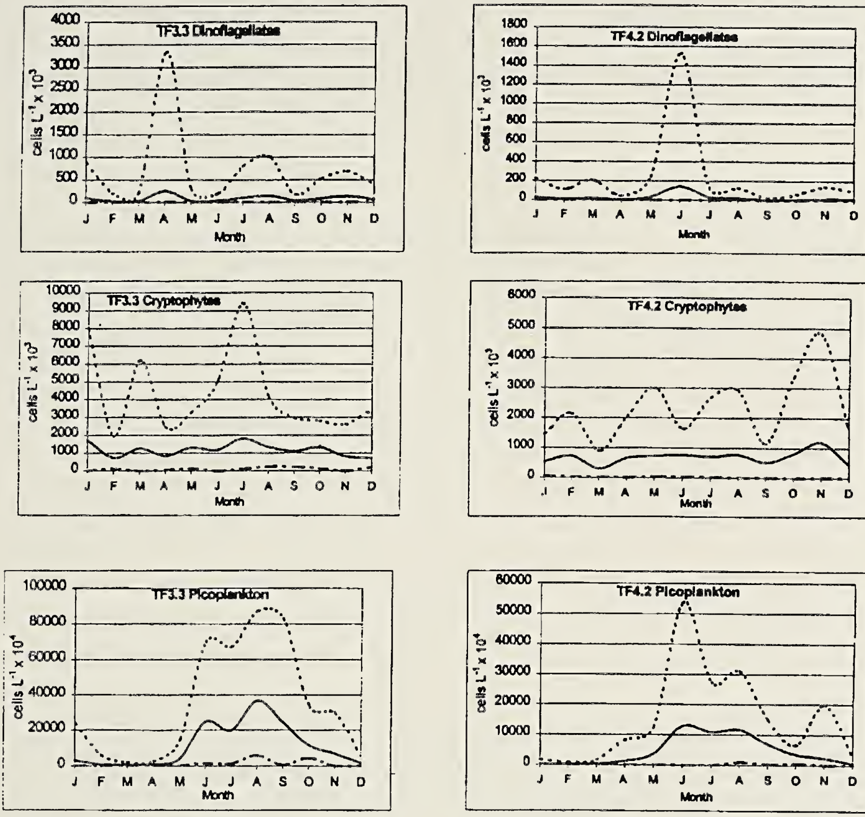

FIGURE 7. Monthly concentrations for dinoflagellates, cryptophytes, and autotrophic picoplankton at stations TF3.3 and TF4.2, 1986-1999, indicating mean (solid line), maximum (dotted line), and minimum (dot-dash line) records.

rivers (Marshall and Nesius, 1993). The greatest development and diversity within this category occurred during the more stable, decreased flow periods of the year (summer, early fall), which also coincided with warmer water temperatures and a reduced sediment load.

3. Chlorophyceae

The chlorophytes were among the most common taxa in the tidal freshwater region. They consisted of a diverse group of single cell, or small colonial forms in the Pamunkey (57 taxa) and Rappahannock Rivers (52 taxa). Seasonal maxima were greater at the Rappahannock River station, and developmental patterns also differed in the two rivers (Figure 6). At TF3.3, several seasonal peaks occurred in late spring, mid-summer, and early fall. The mean monthly range of cells varied from 0.5 to 2.7 x 10^6 cells L^{-1} (April, July), with a maximum of 19.6 x 10^6 cells L^{-1} in July. At TF4.2 lower concentrations prevailed, with the mean monthly abundance from 0.08 to 2.2 x 10^6 cells L^{-1} (March, July), with a maximum of 11.0 x 10^6 cells L^{-1} for September. At TF4.2 there was a single development during summer, rather than several peak periods

present at TF3.3. Taxa most prevalent included a diverse group of *Scenedesmus* spp, *Ankistrodesmus falcatus, A. falcatus v. fluviatile, Pediastrum duplex*, plus several *Crucigenia* spp. and desmids. *Scenedesmus quadricauda* was recorded year round, but also common were *S. bijuga, S. dimorphus*, and *S. acuminatus*, with the filamentous *Ulothrix variabilis* also abundant. The development of these taxa favored the less turbulent conditions in the rivers between the spring rains and the fall-winter period.

4. Dinophyceae:

Dinoflagellates were not abundant at these stations. Ten species common for this region were recorded and included the freshwater *Peridinium cinctum, P. wisconsinense* and *Ceratium hirundinella*, plus several taxa characteristic of the downstream estuarine waters, e.g. *Heterocapsa rotundata, H. triquetra,* and *Prorocentrum minimum* (Marshall and Affronti 1992). There were differences in their abundance, presence, and seasonal patterns at the two stations (Figure 7). TF3.3 contained the higher mean concentrations, exhibiting abundance peaks in spring, summer, and late fall, with lowest concentrations during the winter months when freshwater status was more common. The range was from 0.03 to 0.25 x 10^6 cells L^{-1} (February, April), with a maximum abundance of 3.3 x 10^6 cells L^{-1} for April. At TF4.2 the cell maxima occurred in early summer, with a maximum count of 1.5 x 10^6 cells L^{-1} in June, and monthly ranges from 0.004 to 0.14 x 10^6 cells L^{-1} (September, June), with late winter and mid-spring lows prevailing. These taxa were absent in numerous samples throughout the year and most common at TF3.3.

5. Cryptophyceae:

Although represented by a modest number (5) of species, this was a ubiquitous group throughout the year. There were seasonal fluctuations of development at both stations, with greater abundance at TF3.3 (Figure7). Mean monthly concentrations ranged from 0.7 to 1.8 x 10^6 cells L^{-1}, and 0.3 to 1.2 x 10^6 cells L^{-1} at TF3.3 and TF4.2 respectively. Maximum records for these two stations were 9.4 and 3.4 x 10^6 cells L^{-1} in July and November for TF3.3 and TF4.2. The cryptophytes have been noted as a common background population to other flora within Virginia tributaries (Marshall and Alden 1990). The species recorded were *Cryptomonas erosa, C. marsonni, C. ovata, C. reflexa*, and *Rhodomonas minuta.* The major cryptomonad development was from early spring through mid-fall, and then decreased in early winter to a mid-winter low.

6. Autotrophic picoplankton:

Ubiquitous throughout the year, this category consisted of mainly isolated single cells, or those in small doublets of cells. Cells in this category were less than 2.0 microns in size and did not include species reported in the other categories. They consisted of mainly cyanobacteria and less abundant chlorophytes, with other eucaryotes occasionally present, but not dominant. Maximum concentrations occurred during the summer months (July-September), but these high numbers frequently extended into early fall and were similar to patterns described in these rivers and Chesapeake Bay (Marshall and Affronti, 1992; Marshall, 1995). The mean monthly ranges for TF3.3 were from 8.3 to 367 x 10^6 cells L^{-1} (March, August), and for TF4.2 from 2.2 to 128.2 x 10^6 cells L^{-1} (February, June), with maxima for these two stations at 870 and 537 x 10^6 cells L^{-1}

(August, June) (Figure 7). The minimum counts were 0.31 and 0.18 x 10^6 cells L^{-1} (December, March) at TF3.3 and TF4.3 respectively. The seasonal maxima occurred during the summer/fall months, being associated with warmer water temperatures and reduced river flow, in addition to being a major contributor to productivity during this period (Marshall and Nesius, 1993).

7. Other Phytoplankton Categories:

Among other algal categories, there was a small variety of additional background taxa that included euglenophytes, xanthophytes, and chrysophytes. These groups were generally not abundant, with low species diversity in both rivers, and were more common during the summer/fall months. Representative xanthophytes were *Centritractus belonophorus, Ophiocytium cochlerare, Tetraedriella spinigera, Tribonema minus, T. affine*, and *T. viride*. The common euglenophytes were *Euglena acus, Lepocinclis* sp., *Phacus caudatus, P. longicauda, Strombomonas asymmetrica, S. affinis*, and *Trachelomonas hispida*. The chrysophytes were less abundant, but more diverse, and included *Dinobryon cylindricum, D. sertularia, D. sociale, Synura uvella, Ochromonas minuscule, Chrysococcus ornatus*, and *Chromulina wislocchiana*. These taxa were noted sporadically within the samples, lacking established periods of major development.

DISCUSSION

The tidal freshwater region of these rivers contained a diverse representation of phytoplankton taxa dominated in abundance and biomass by a diatom flora. High concentrations of the diatoms occurred during winter-spring, summer, and fall, with decreasing abundance in early winter. Although representative taxa from the other algal categories were present throughout the year, their development was most pronounced in summer and early fall. The patterns of development coincided with periods of high and low river flow. The maximum and minimum concentration records for the different algal categories provide a graphic illustration of the variability that may exist in their development. The major physical influence on water flow during these seasons was the period of the spring rains and increased flow within these rivers, which was followed by months of reduced flow and increased residence time for flora passing through the tidal regions of these rivers. Although the general phytoplankton composition and the dominant species at these stations were similar and of mainly freshwater origin, there were differences in water quality and the abundance of the algal flora. For instance, station TF3.3 (Rappahannock River) represented waters with a more rapid rate of flow from a larger drainage system than TF4.2 (Pamunkey River), plus the total suspended sediment loads were greater, and mean Secchi readings were less at station TF3.3, in comparison to TF4.2. The total phosphorus values were somewhat similar, in what may be considered a nitrogen limiting system for both river stations (low TN:TP ratios predominated). The mean spring and fall chlorophyll pulses at TF3.3 corresponded to higher levels of TN and TP, with the summer chlorophyll highs associated with increased TP levels and a decrease in TN. These periods coincided with the spring diatom pulse, followed by increased abundance of cyanobacteria and chlorophytes during the summer, with a resurgence of diatom concentrations in fall. These were similar to patterns noted in the nearby James River (Marshall and Affronti, 1992; Marshall and Burchardt, 1998). Chlorophyll concentrations typically decreased with

the lower temperatures of winter. At TF4.2, the greatest concentrations of chlorophyll were in summer, along with increased levels of both TN and TP. The mean TN:TP ratios increased during greater water flow within the rivers, when additional nitrogen input occurred, and followed by increased diatom development. The decreased flow of summer was associated with increased residency time, lower levels of TSS, deeper Secchi readings, increased picoplankton, increased productivity, greater species diversity, greater abundance of chlorophytes and dinoflagellates, plus higher chlorophyll concentrations. This was in contrast to the reverse status of these variables associated with the increased flow rates during the winter/spring months.

In contrasting the flora at these stations, the Pamunkey River contained a greater diversity of diatoms, cyanobacteria, chlorophytes, chrysophytes, cryptophytes, and euglenophytes. Of the 268 taxa identified at these two stations, 232 (86.6%) were recorded in the Pamunkey River, with 208 (77.6%) in the Rappahannock River, and there were 61.9% of the taxa common to both stations. Differences in composition were mainly noted in three algal categories (diatoms, dinoflagellates, chlorophytes), with additional estuarine species recorded at TF3.3. There was greater phytoplankton abundance, productivity, and biomass in the Rappahannock River (TF3.3), which also contained higher TN and TP concentrations, with indications of less light availability than station TF4.2, as indicated by the more shallow Secchi depths recorded.

SUMMARY

The comparison of the tidal freshwater regions of two closely located river systems indicated both differences and similarities in the abundance, diversity, and development of the phytoplankton populations. These differences, which include the ranges of seasonal and annual development among the various phytoplankton taxa, were a product of the unique combination of conditions in the two rivers (e.g. water quality, light and nutrient availability, seasonal flow rates). These cumulative factors, and others, influenced the floral composition and its seasonal abundance, plus determine the initiation and duration of development among the algal assemblages. These conditions were further influenced by the amount, timing, and duration of river water flow annually, when wet and dry years of water occur within these rivers. Yet, there were similarities in algal composition and dominant species within these rivers, and in their seasonal development transitions that extend beyond local conditions and are characteristic of broader developmental patterns typically associated with phytoplankton in temperate regions.

ACKNOWLEDGMENTS

This study is a component of the Chesapeake Bay Monitoring Program supported by the Virginia Department of Environmental Quality and the U.S. Environmental Protection Agency. Special thanks are given to Dr. Kneeland Nesius of Old Dominion University for providing the results of the productivity analysis determined during the period of study. Both authors participated in the species identification and data analysis of this paper.

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Virginia Journal of Science
Volume 56 Number 2
Summer 2005

The Small Mammals of Isle of Wight County, Virginia, as Revealed by Pitfall Trapping,

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ABSTRACT

In a study conducted in mid-winter, pitfall traps were used to assess the small mammal communities on 14 grids set in open habitats in Isle of Wight County in eastern Virginia. In all, 136 shrews of three species and 103 rodents of five species were trapped. Least shrews (n=110) comprised 46 percent of small mammals and 80 percent of shrews. Eastern harvest mice (n=62) were the most common rodents. Reproduction was detected only in pine voles and southern bog lemmings. The majority of small mammals of the region were trapped during this month-long study.

INTRODUCTION

As part of a study to determine the western extent of populations of the then federally threatened Dismal Swamp southeastern shrew, *Sorex longirostris fisheri*, I conducted a survey of small mammals in Isle of Wight County, located just west of the City of Suffolk and lying approximately 40 km west of the Great Dismal Swamp National Wildlife Refuge in eastern Virginia. Using a standard protocol to study the Dismal Swamp southeastern shrew, an assistant and I established 14 study grids at different locations throughout the county. Trapping between 6 January and 6 February 1992, we collected 239 small mammals of eight species. This report relates the details of the types of small mammals, and their associations, in a coastal plain county in eastern Virginia.

MATERIALS AND METHODS

The southeastern shrew, the species of particular interest, is known to achieve greatest numbers in early successional habitats, such as oldfields, recently clearcut forests, and sites that are infrequently mowed (Rose et al. 1990). Powerline rights of way provide excellent habitat for such small mammals because they are mowed at 3-5 year intervals to prevent excessive growth of shrubs and trees, thereby continually setting back biological succession and promoting the persistence of perennial grasses and other herbaceous plants. Furthermore, because powerlines cross roadways, these habitats are easily reached, an additional benefit. Several high-voltage powerlines form a network across Isle of Wight County (Figure 1), many radiating from the Surry Nuclear power plant located on the south side of the James River. Thus, wherever county roads crossed the 30 m wide powerlines, I examined the vegetative stage of the habitat and usually was able to establish one or two study grids nearby.

The trapping grids were placed on sites with vegetation that is typical of early succession in the region. Grasses, mostly in the genera *Andropogon, Panicum*, and *Uniola*, dominated the vegetation of most grids, but sedges (*Carex* spp.) and even softrushes (*Juncus* spp.) were present on wetter places. Many grids had American cane (*Arundinaria gigantea*) and other woody elements, such as brambles (*Rubus* spp.), Japanese honeysuckle (*Lonicera japonica*), and tree seedlings, especially of sweet gum

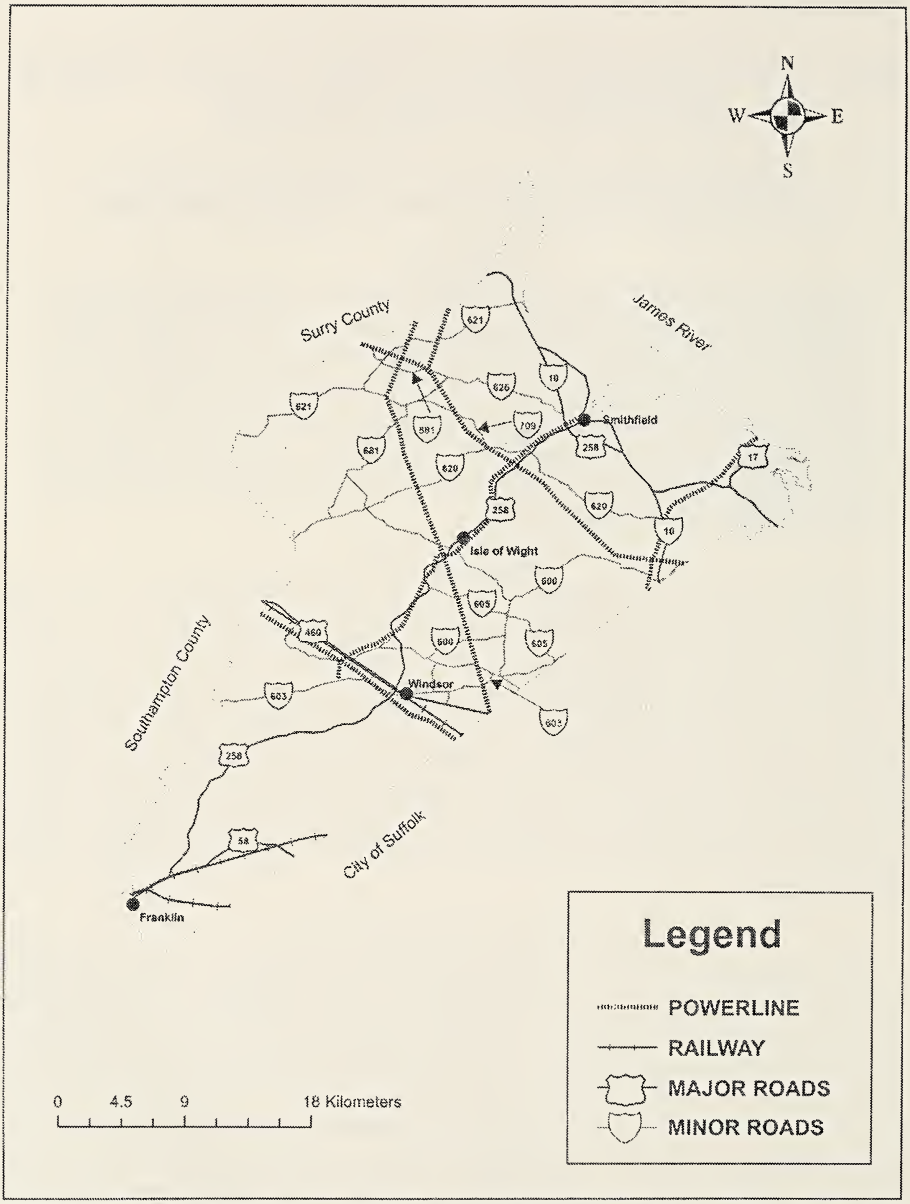

FIGURE 1. Map of Isle of Wight County, Virginia, showing the state roads and powerlines relevant to this study. The study grids were placed near where powerlines crossed the state roads, at locations listed in Table 1.

(*Liquidambar styraciflua*). The soils varied greatly among the 14 sites with grids, from sandy loams to silty clays, and occasional patches of black or peaty loams.

The standard trapping protocol for our shrew studies used a 5 X 5 grid with 12.5 m intervals, covering an area of 0.25 ha. Near each coordinate, we dug a 15 cm diameter hole, deep enough to accommodate a 15 X 23 cm #10 tin can. When partly filled with water or formalin solution, these serve as efficient pitfall traps, a common method to

secure some species of small mammals, especially southeastern shrews, that are resistant to being trapped by live or snap traps. These pitfall traps were unbaited, because early studies demonstrated that baiting did not increase their efficiency (Hudson and Solf 1959).

Once in place, we tended these traps twice a week to remove the bodies of small mammals that had fallen into the traps and drowned. (Drowning is considered to be a more humane method of kill-trapping than other methods, and we sought *Sorex* shrews whose body lengths we could measure). We trapped each grid for three weeks, and then removed all pitfalls from the ground. Earlier studies (Everton 1985) had indicated that little additional information is learned on the small mammals of a site if trapping continued beyond three weeks. Catch rates for pitfall traps tend to be very low, often on the order of 1-2 captures per 100 nights that a trap is in the ground.

Animals were frozen until they could be measured, weighed, and examined for reproductive status. At necropsy, each animal was weighed and then measured for total length and lengths of tail, ear, and hind foot. Each animal was examined for evidence of past or current reproduction (for females) or for current reproductive competency for males (the presence of convolutions in the cauda epididymides of the testes). All cataloged specimens were donated as skeletal material to the Mammal Division of the Smithsonian Institution in Washington, D. C. Because the field study was conducted in the dead of winter, I did not expect to see evidence of reproduction in most species.

RESULTS

In all, 239 small mammals of eight species were collected from the 14 grids in this study (Table 1). The number of specimens per grid ranged from 3-51 and the number of species per grid ranged from 2-6. Least shrews (*Cryptotis parva*) and eastern harvest mice (*Reithrodontomys humulis*) were taken on 13 of 14 grids, whereas the white-footed mouse (*Peromyscus leucopus*) and pine vole (*Microtus pinetorum*) were least common, from one and two grids, respectively. The short-tailed shrew (*Blarina brevicauda*), from seven grids, and southeastern shrew (*Sorex longirostris*), from six grids, also shared locations with least shrews on three grids. The microtine rodents, meadow voles (*Microtus pennsylvanicus*) and southern bog lemmings (*Synaptomys cooperi*), were present on seven and eight grids, respectively, and co-occurred on four grids.

The 239 small mammals collected in this study were taken in 3,750 trap-nights (one trap in place for one night equals one trap-night), for an overall capture rate of 3.25 small mammals per 100 trap-nights. The catch rates among grids ranged from 0.57 to 9.75/100 trap-nights (Table 1), indicating great variation in the densities of populations in the small mammal communities from location to location. There were no obvious vegetation or soil patterns that would account for this range of variation in small mammal abundance among the 14 grids.

Information on the number of specimens, their standard measurements, and other details is presented in Table 2 for the six species with sufficient specimens to permit calculations of standard statistics. Sex ratios of all species did not differ significantly from 1:1, nor was there statistically significant sexual size dimorphism. The mean number of species taken per grid was 4.07 and the mean number of individuals per grid was 17.07, but there was no significant correlation between the number of species and

TABLE 1. Results of pitfall trapping on 14 study grids in Isle of Wight County, Virginia. Grids were placed where state highways or other state roads intersected with high-voltage powerlines. Two grids were placed near state road 600, and three grids each were placed near state roads 621 and 626. "# sites" denotes to the number of sites yielding individuals of that species, "total N" refers to the total individuals of that species collected during the study, and "t-n" equals trap nights.

	Route 10	600/1	600/2	603	605	620	621/1	621/2	621/3	626/1	626/2	626/3	681	709	# sites	total N
Blarina brevicauda	1	3	2			2			3	2				1	7	14
Cryptotis parva	1	2	10		6	3	5	5	36	4	9	12	6	11	13	110
Sorex longirostris	1		2		3				2		3		1		6	12
Peromyscus leucopus				2											1	2
Reithrodontomys	5	4	2	1	16	3	4	3	7		5	5	3	4	13	62
Microtus pinetorum	1													1	2	2
M. pennsylvanicus	4						2		3	1	3	2	2		7	17
Synaptomys cooperi		4	2		4	1	1	1		1			6		8	20
Total individuals	13	13	18	3	29	9	12	9	51	8	20	19	19	16		239
Total species	6	4	5	2	4	4	4	3	5	4	4	3	6	3		
Catch rate/100 t-n	2.47	2.47	3.42	0.57	5.52	1.71	2.28	1.71	9.75	1.52	3.80	3.61	3.61	3.02		

number of individuals across the 14 grids (r = 0.337, P = 0.24). Thus, grids that yielded more individuals did not have more species than grids with few individuals.

Because this study was conducted in mid-winter, most of the animals collected were full adults and exhibited little evidence of reproduction. Exceptions were seen only in pine voles (female with five embryos and male was fertile) and southern bog lemmings, in which 15 g male and 18 g female, both late juveniles based on body size, were taken, plus two females were pregnant and all males of adult size were judged to be fertile. In all other species, the minimum sizes were those of adult animals (Table 2), and no evidence of reproduction was detected.

DISCUSSION

The three shrews and five rodents represent the majority of small mammals that are typical for the region. The shrews are all of the common ones; only the pygmy shrew, *Sorex hoyi*, was absent, and this tiny shrew has a patchy distribution, usually in shrubbier or more forested habitats than were examined in this month-long study of small mammals in the open habitats under powerlines. Among the rodents, only the introduced house mouse (*Mus musculus*) was absent among the mammals small enough to be contained by the 23 cm tall pitfall traps used in this study. House mice, introduced from Europe to the Americas during colonial times, are excellent colonizers of newly created and early successional habitats, but they tend to disappear once natural plant communities required to sustain native mammal populations have developed. Those conditions seemed to apply here. The hispid cotton rat, *Sigmodon hispidus*, likely was present on some grids but adults are too large to be caught in pitfall traps. The only other common small mammal in the region, the marsh rice rat (*Oryzomys palustris*), is associated with wet or regularly flooded sites, and thus was unlikely to be present on these mostly mesic sites.

The short-tailed shrew (*Blarina*) is perhaps the most common and widespread small mammal, and certainly is the most common shrew, in eastern North America. Tolerant of a wide range of conditions and thus found in habitats ranging from moderately dry oldfields to wet closed forests, this shrew is the largest North American shrew. The 14 collected in this study averaged 13 g (Table 2). Half the grids yielded short-tailed shrews, but only 1-3 individuals each, indicating that they were never as numerous as least shrews on these sites.

Short-tailed shrews have been studied extensively for their adaptations that enable them to sustain their high metabolic rates year round (no American shrew hibernates). For example, Merritt (1986) reports that this shrew possesses brown adipose tissue, a special fat that, when required, produces heat under stimulation from the adrenal gland. In effect, this is a supplementary or emergency source of heat production to that of shivering, the normal manner by which mammals produce heat on demand to get their sagging body temperatures back into the normal range. Their high metabolic rates also contribute to their remarkable abilities to produce young strictly through maternal energy sources during pregnancy and lactation. Pearson (1944) reports that an 11 g *Blarina* produced five weaned young that collectively weighed 55 g in just 50 days: 21 days for pregnancy and the rest for lactation. Two species of shrews in the genus *Sorex*, studied by Nagel (1994) in Germany, show a similar ability, producing young during pregnancy and lactation that were equivalent to 536 and 540 percent of the initial body weights of the mother shrews. Thus, besides an ability to mobilize sufficient

TABLE 2. The means, standard errors of means, minimal and maximal measurements for total length, tail length, weights, and the sample sizes for six species of small mammals taken in pitfall traps in Isle of Wight County, Virginia. Too few *Microtus pinetorum* and *Peromyscus leucopus* were caught to include in this table.

		MALES			FEMALES		
		Total length mm	Tail length mm	Weight (g)	Total length mm	Tail length mm	Weight (g)
Blarina	Mean	115.0	25.57	14.26	114.43	26.86	12.34
brevicauda	SE	2.49	0.75	0.56	1.64	1.26	0.32
	Min	109.0	22.0	11.71	110.0	23.0	11.50
	Max	127.0	28.0	16.40	123.0	31.0	13.61
	N	N=7			N=7		
Cryptotis	Mean	78.41	17.70	3.88	77.70	18.17	3.91
parva	SE	0.71	0.21	0.07	0.48	0.20	0.08
	Min	67.0	13.0	1.80	66.0	15.0	2.03
	Max	97.0	21.0	5.33	87.0	21.0	5.25
	N	N=56			N=64		
Sorex	Mean	89.86	34.57	3.08	88.75	33.50	3.15
longirostris	SE	0.70	0.65	0.27	0.22	0.25	0.11
	Min	88.0	33.0	1.74	88.0	33.0	2.80
	Max	93.0	38.0	3.95	89.0	34.0	3.56
	N	N=7			N=5		
Reithrodontomys	Mean	122.56	58.66	8.58	118.57	56.47	7.94
humulis	SE	1.44	0.92	0.19	1.72	0.87	0.29
	Min	109.0	49.0	6.21	105.0	48.0	4.19
	Max	140.0	69.0	12.03	140.0	68.0	11.41
	N	N=32			N=30		
Microtus	Mean	147.0	43.50	31.26	148.29	41.29	31.7
pennsylvanicus	SE	6.64	2.43	3.68	3.22	1.06	2.09
	Min	112.0	32.0	13.10	131.0	36.0	21.87
	Max	167.0	52.0	45.08	154.0	45.0	40.12
	N	N=10			N=7		
Synaptomys	Mean	118.54	20.69	27.96	128.86	23.0	32.17
cooperi	SE	2.44	0.86	2.09	4.72	2.90	3.79
	Min	102.0	15.0	14.63	117.0	18.0	24.05
	Max	129.0	26.0	41.63	151.0	40.0	47.36
	N	N=13			N=7		

energy to maintain a constant body temperature, female shrews are able to find additional energy from food to produce young equal to five times their own body weight in just 7-8 weeks. Because young shrews do not leave the nest to forage as juveniles but stay in nests until weaned at 95 percent of adult weight, their entire body weight gain after birth must come from the milk they acquire from their mothers.

The least shrew, the only brownish short-tailed shrew in Virginia, was the most numerous small mammal, with 56 males and 64 females (Table 2) collected from 13 of 14 grids (Table 1). Thus, they comprised 46 percent of total mammals. This shrew, at least in eastern Virginia, is mostly restricted to dry sites with mineral soils (Everton 1985). At less than 4 g in body weight, this is one of the dozen smallest mammals in the world. The number of least shrews per grid was highly variable, ranging from 1 or 2 to 9, 10, 11, to as many as 36. Distributed throughout Virginia in appropriate habitats, the highest densities have been reported by Adkins (1980) from tidal marshes on the Eastern Shore, specifically of Assateague Island. Least shrews are more social than other shrews, often forming groups. Jackson (1961) reports finding "about 25 shrews" in a leaf nest in Virginia and McCarley (1959) describes the well-insulated nest in which he found "at least 31 shrews" in early January in eastern Texas.

The southeastern shrew, the primary subject for which this study was undertaken, was found on 6 of 14 grids, always in low numbers (1-3 per grid). All were similar in size, weighing < 4 g and measuring nearly 90 mm in body length (Table 2). The most common long-tailed shrew in eastern Virginia, it is slightly longer and heavier than the pygmy shrew. Longer shrews of the Dismal Swamp subspecies, *Sorex longirostris fisheri*, ranging in body length to near or slightly above 100 mm, are found mainly in wet sites with peaty soils, whereas the upland subspecies, *S. l. longirostris*, is somewhat smaller, with lengths in the low to mid-80s mm range (Everton 1985). Three of the six grids yielding southeastern shrews also had the other two shrew species present as well. Before the regular use of pitfall traps, the southeastern shrew was considered to be one of the rarest American shrews throughout its distribution in the southeastern states. Many of the first or second state records were of specimens found dead on trails, dug from nests in rotting logs, or found floating in water-filled stumps or receptacles at the bottom of downspouts. However, with the systematic use of pitfall traps, initially by French (1980), southeastern shrews often are the most numerous small mammal species of a site. This result also was found to be true in eastern Virginia (Everton 1985), especially on wet or damp sites.

The white-footed mouse, *Peromyscus leucopus*, is a forest-dwelling arboreal rodent that occasionally is present in early successional sites. The two specimens collected on the grid near state road 603 were sub-adults in gray pelage, and likely were animals dispersing from one nearby forest to another. The white-footed mouse is considered the most common rodent in forests in eastern North America.

The eastern harvest mouse, *Reithrodontomys humulis*, was by far the most numerous rodent, with 62 being taken on 13 of the 14 grids (Table 1). These 62 harvest mice represented 60 percent of all rodents and 25 percent of all specimens taken in the study. The number per grid was usually small, five or less but two grids yielded 7 and 16 specimens. The smallest rodent in eastern North America (< 10 g), harvest mice eat insects and seeds and build aerial nests in tufts of grasses. Only pregnant females exceed 10 g. This nocturnal species often is numerous on sites with tall herbaceous vegetation, such as was present on most of the grids. Cawthorn and Rose (1989), who studied the

dynamics of a population of eastern harvest mice in similar oldfield habitat in Portsmouth, Virginia, found densities to be some of the highest of any harvest mouse in North America, so their ubiquity and numbers are not surprising in the present study. Harvest mice are often found in association with hispid cotton rats, a species almost always the largest rodent in the same oldfields (Cameron 1977; Cameron et al. 1979; Joule and Cameron 1975; Rose pers. obs. in southern Chesapeake in an on-going study). The reasons for this association remain to be revealed.

The other three small mammals are short-eared, short-tailed animals in the subfamily Microtinae of the Order Rodentia. Most microtine rodents have the common names of voles and lemmings, but the muskrat (*Ondatra zibethicus*) is the largest member of this group of strict herbivores. Microtines are intermittently active day and night, have high metabolic rates, and are exceedingly efficient at turning grass into flesh. Sometimes microtines breed year-round (even in the arctic!) and so members of this group had the greatest potential to exhibit reproduction during this study, conducted in mid-winter.

The meadow vole flourishes in grassy fields, wet or drier, and is considered the most common and widespread herbivorous rodent in eastern North America. I caught 17 on seven grids, usually in low numbers (1-4 per grid). Many grids had too little covering vegetation to support populations of meadow voles: some studies indicate that 90 percent covering vegetation is required (review by Getz 1985). Before the arrival of hispid cotton rats into Virginia in 1940 or slightly before (Patton 1941), the meadow vole was the largest rodent in grassland or early successional habitats and as such was the staple in the diets of snakes and carnivorous mammals and birds. Meadow voles build runways through grassy vegetation, which they maintain by clipping the vegetation that grows in their footpaths. They frequently build feeding runways off the main trails, and there they sit on their haunches and, using their sharp incisors, cut the grasses into 3-5 cm sections until they get to the most palatable and nutritious bits, which they consume. Thus, their presence can often be told by the small piles of cut vegetation in runways. In the winter, they are able to sustain themselves by eating, if necessary, dead and dried grasses and by conserving energy during their hours of inactivity in well-insulated subterranean nests.

The pine vole, also sometimes and more appropriately called the woodland vole, is a smaller and shorter-tailed version that lives in early successional habitats but more typically at low densities in woodlands. Thus, its habitat requirements or tolerances are broader than those of the meadow vole. Unlike the brownish black and scruffy-haired meadow vole, the pine vole has a short velvety pelage of a uniform chestnut-brown color. Its tail is only as long as its hind foot, compared to the tail of the meadow vole, which is twice as long as the hind foot. Pine voles, which build shallow burrow systems 3-5 cm below the surface, sometimes are economic pests, especially in orchards, because they eat the bark off the root systems of trees and shrubs, sometimes girdling and killing the plant. The pine vole is present in low densities in mature forests throughout its range in eastern North America, but often reaches higher densities in early successional habitats, such as recently clearcut forests. In the present study, only one male and one female were collected, on separate grids. Called the pine vole because the specimens from which the species was described and named came from pine forests in South Carolina, we now know that pine voles are rare in pine forests and much more abundant in deciduous forests, hence the alternative common name of woodland vole.

Finally, perhaps the most interesting small mammal to be collected was the southern bog lemming. Similar in size and proportions to the pine vole but with a grizzled grayish pelage and a squarish nose with its exceedingly long and 'busy' nasal whiskers, this species generally is thought to require wetter habitats than the other microtine rodents (as the common name suggests). In Virginia, the southern bog lemming is found in some cool wet habitats in the montane west, such as in Montgomery and Giles counties near Blacksburg, but an isolated subspecies, *Synaptomys cooperi helaletes*, is known only from the Dismal Swamp region. Until I caught several in pitfall traps in the Great Dismal Swamp National Wildlife Refuge in early 1980 (Rose 1981), some investigators (such as Handley 1979) speculated that this subspecies might be extinct. The southern bog lemming is another species rarely caught in live or snap traps (Rose et al. 1990; Stankavich 1984), but pitfall trapping studies have revealed it to be widespread and locally common in some locations. In this study, I collected 20 southern bog lemmings on 8 of the 14 grids, making it more numerous and widespread than either species of *Microtus*. Most of the grids yielded one or two specimens but two grids yielded four and one six specimens. The results of this study show that the Dismal Swamp southern bog lemming is flourishing beyond the bounds and habitats of the Dismal Swamp.

Among the small mammals collected in this mid-winter study, evidence of reproduction was seen only in pine voles and southern bog lemmings. The lone female pine vole had five embryos and the male was judged to be fertile, based on the presence of sperm in the cauda epididymides. Two southern bog lemmings were pregnant, and all adult-sized males were judged to be fertile. That winter breeding occurred is also supported by the two juvenile southern bog lemmings taken in the pitfall traps. Surprisingly, no female meadow vole was pregnant and all males were judged to be infertile. No embryos were found in any species of shrew or in harvest mice, so only the southern bog lemming and pine vole were reproducing over the winter.

In conclusion, the small mammals of Isle of Wight County presented few surprises, except perhaps the widespread presence and abundance of least shrews and the presence of southern bog lemmings so great a distance from the Dismal Swamp. It seems likely to me that southern bog lemmings will be found even farther westward from the Dismal Swamp, provided that searches using pitfall traps are made in appropriate habitats.

ACKNOWLEDGMENTS

I thank John Rose for field assistance, ODU undergraduate Sharon Sockman for help with measuring, necropsying, and tallying the small mammals, Scott Bellows for preparing the figure, and the non-game program of the Virginia Department of Game and Inland Fisheries for their support of my studies of southeastern shrews in eastern Virginia.

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Virginia Journal of Science
Volume 56 Number 2
Summer 2005

Bats Of Skydusky Hollow, Bland County, Virginia

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ABSTRACT

During the period 22 November 1999 – 11 October 2001, winter hibernacula surveys, spring staging/autumn swarming surveys, and summer surveys for bats were completed in caves of Skydusky Hollow, Bland County, Virginia. During winter, 12 caves were entered and 16,185 bats counted: 235 *Myotis sodalis* (Indiana bat), 14,475 *Myotis lucifugus* (little brown myotis), 12 *Myotis septentrionalis* (northern myotis), 7 *Myotis leibii* (eastern small-footed myotis), 1,441 *Pipistrellus subflavus* (eastern pipistrelle), and 15 *Eptesicus fuscus* (big brown bat). *Myotis sodalis* hibernated in thermally stable areas of 7 - 9°C. The largest concentration of *M. lucifugus* (n = 4,280) hibernated in an area that was cooler (6.5°C) than areas used by *M. sodalis*. The remaining 6,300 *M. lucifugus* hibernated at temperatures similar to, or slightly cooler than, temperatures used by *M. sodalis*. Intra-cave (and possibly inter-cave) movements of *M. lucifugus* and *M. sodalis* during the season of hibernation concentrated bats in cooler areas of the caves. An unusually large concentration of *P. subflavus* (n = 920) hibernated in Coon Cave in a warm (8.6 – 9.7°C), stable environment. Proportions of species of bats captured during spring staging and autumn swarming varied from proportions found during winter hibernation. Mating and perhaps other social functions affect patterns of autumn use. No concentration of bats used the caves during summer.

INTRODUCTION

The association between bats and caves is well known. Although a few species of bats from temperate regions use caves during summer, use of caves as hibernacula is more common. Winter ranges of many species, including federally endangered *Myotis sodalis* (Indiana bat) and *Corynorhinus townsendii virginianus* (Virginia big-eared

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bat), are restricted to areas of well-developed karsts such as are found in western Virginia (Barbour and Davis 1969).

Few studies have examined use of a cave or cave system by bats across seasons. In addition to hibernation, bats use caves in other ways. Autumn swarming is a phenomenon exhibited by microchiropterans in North America (Cope and Humphrey 1977) and Europe (Parsons et al. 2003). Swarming is the use and visitation of hibernacula and nearby habitats in late summer and early autumn, and for many species swarming is associated with the opportunity for sexes to meet and mate (Cope and Humphrey 1977; Thomas et al. 1979; Parsons et al. 2003). During spring staging, bats often remain near hibernacula caves for a few days before leaving for summer maternity areas. In summer, some species, for example *C. t. virginianus* and *Myotis grisescens* (gray myotis), form maternity colonies in warm areas of caves (Barbour and Davis 1969), or caves may be used by a bachelor colony (LaVal and LaVal 1980), a loose aggregation of males, of these species. Bats sometimes also use caves as stopovers during the spring and autumn migration/transient period (Parsons et al. 2003), and bats visit a variety of habitats and situations during all seasons, apparently searching for suitable habitat (Fenton 1969; Kurta et al. 2002).

We studied bat use of caves of the Skydusky Hollow Cave System and other nearby caves within the same karst system in Bland County, Virginia. Studies included (1) surveys for hibernating bats, including temperatures used by concentrations of bats, winter intra-cave movements, and a search for accumulations of guano that indicate summer nursery use, (2) spring staging and autumn swarming, and (3) a summer survey for nursery colonies.

Background on bat populations.—Unpublished data from previous visits to Skydusky Hollow caves by several individuals influenced the design and completion of our studies. These data (Table 1) provide background information that might otherwise be lost. A group of cavers organized by authors Carol and Joe Zokaites completed a bat count in five caves of Skydusky Hollow on 8 February 1992 when 7,470 bats were found, providing background information on portions of caves where bats concentrate during winter. Winter visits have been made to Newberry-Bane Cave by many individuals. In 1986, probably from the Bane entrance, Ginny Dalton (Radford University, personal communication) found 159 bats of 5 species, including two endangered species: *C. t. virginianus* and *M. sodalis* (Table 1). On each of four visits (1990, 1992, 1995, and 1999) Gary Nussbaum and students (Radford University, personal communication) reported from 120 to 4,203 bats of 1 to 6 species (Table 1). In 1993, author Richard Reynolds, Chris Hobson (Virginia Department of Conservation and Recreation), and colleagues surveyed from both Newberry and Bane entrances and found six species of bats, and recorded for the second time the presence of *C. t. virginianus*.

MATERIALS AND METHODS

Study area.—The Skydusky Hollow Cave System is in Walker Creek Valley between Brushy and Big Walker mountains, Bland County, in western Virginia, about 90 km west of Roanoke. It is in the Valley and Ridge Physiographic Province, with elevations of 649 - 1,160 m. The Skydusky Hollow Cave System includes, from west to east, Coon, Paul Penley (and Harmans Avalanche Pit), Buddy Penley, Newberry-

TABLE 1. Unpublished data of bats found during previous winter surveys of caves in Skydusky Hollow, Bland County, Virginia. Bats counted but not identified to species are recorded as Unknown. When species identification was tentative, the name is followed by (?).

Year	Cave	Location in Cave	No. of bats by Species
1986[1]	Newberry-Bane		4 *C. t. virginianus*
			90 *M. sodalis*
			2 *M. leibii*
			1,800 *M. lucifugus*
			62 *P. subflavus*
1990[2]	Newberry-Bane		120 *M. sodalis*
			90 *M. lucifugus*
			6 *M. septentrionalis*
			4 *E. fuscus*
			11 *P. subflavus*
1992[3]	Paul Penley	Whisper Hall	524 - Unknown
		Big Room	138 - Unknown
		South of Big Room	135 - Unknown
		Victory Room	122 - Unknown
		Upper Level	121 - Unknown
		Harman's Metro	280 - Unknown
	Buddy Penley	Entrance Passage	40 *P. subflavus*
			11 *M. lucifugus*
		Main Pit (Pit 1)	3,100 *M. lucifugus*(?)
		Lower Passage	10 *P. subflavus*
			525 *M. lucifugus*
	Bane Spring	Main areas	278 *P. subflavus*
			543 *M. lucifugus*
			5 *E. fuscus*
			3 *M. sodalis*(?)
			1 *M. leibii*
		Back pits	21 *P. subflavus*
			66 *M. lucifugus*
	Spring Hollow	Entrance area	160 Unknown
	Newberry-Bane	Tourist Connection	163 Unknown
		T-Intersection	528 Unknown
		Straddle Pit and	90 *M sodalis*
		Connection area	553 *M. lucifugus*
			63 *P. subflavus*
1992[2]	Newberry-Bane		100 *M. sodalis*
			4,000 *M. lucifugus*
			3 *M. septentrionalis*
			100 *E. fuscus*
1993[4]	Newberry-Bane		5 *C. t. virginianus*
			107 *M. sodalis*
			13 *M. leibii*
			988 *M. lucifugus*
			10 *E. fuscus*
			30 *P. subflavus*
1995[2]	Newberry-Bane		110 *M. sodalis*
			11 *M. leibii*
			8 *M. lucifugus*
			2 *M. septentrionalis*
			6 *E. fuscus*
			9 *P. subflavus*
1999[2]	Newberry-Bane		120 *M. sodalist*

1 Ginny Dalton (Radford University, personal communication)

2 Gary Nussbaum and students (Radford University, personal communication)

3 Data from simultaneous surveys of the caves by a group of cavers organized by Carol and Joe Zokaites

4 Richard Reynolds (Virginia Department of Game and Inland Fisheries), Chris Hobson (Virginia Department of Conservation and Recreation), and colleagues

Bane, Bane Spring, and Spring Hollow caves. These caves are hydrologically connected (Wright 1995), although physical connections have not always been established.

A description and map of the Skydusky Hollow Cave System was provided by Zokaites (1995), and maps of three caves, Newberry-Bane, Buddy Penley, and Paul Penley, were provided by Zokaites and Zokaites (1995) and Devine (1995a, 1995b). Newberry-Bane Cave, largest and most complex of the system, has two entrances, the Newberry and Bane entrances. Where the two entrance passages intersect is a maze of passages referred to as the Junction (area), with Upper and Lower Junction areas. In addition to caves of the Skydusky system, six caves in the same karst system were also surveyed: Munsey #1 and #2, Munsey Twins (#1 and #2 entrances), Morehead's Pit, and Springhouse Cave.

The Skydusky Hollow karst is part of a linear belt of karsts extending from the northwest flank of Walker Mountain northward to Walker Creek Valley, developed in Cambro-ordovician limestone and dolomite. Streams and talus springs draining the north flank of Walker Mountain sink at or near the upper limestone contact, and flow through a complex network of caves before emerging at springs along Walker Creek. Extensive, accessible cave passages are restricted to upper limestone formations that lie beneath or near the upper limestone contact. Sinking streams from east and west ends of the hollow converge in the lowest section of Newberry-Bane Cave.

Hibernacula surveys.—Four caves in Skydusky Hollow were visited 22 - 24 November 1999, to document autumn intra-cave use and to help establish which cave areas, as based on temperature, morphology, and concentrations of bats, were most likely to contain endangered bats during winter hibernation. Winter surveys, 17 January - 5 March 2000, were conducted in areas of 12 caves (1) that contained concentrations of bats, (2) where temperatures were ≤9°C, a range typically suitable for hibernation by concentrations of bats, particularly *M. sodalis*, and (3) that had morphology typical of caves that cool appropriately for hibernation.

Bats were tallied by species and location in the caves. Individuals and bats in small clusters were counted directly, but large clusters of *Myotis lucifugus* (little brown myotis) were estimated in groups of 5 or 10 bats. Searches were made for accumulations of guano, indicative of summer use. Temperatures were taken at cave entrances, in twilight areas, near clusters of endangered bats, near concentrations of other species, and at intervals along the survey route. Temperatures were taken using Raytek infrared thermometer model ST2 or Raynger® ST20, with a range of -18 or -32 to 400°C, an accuracy of ±2 and ±1% of reading, and a display to the nearest 1.0 and 0.2°C, respectively. Brack et al. (2003a) discussed advantages and disadvantages of point and shoot infrared thermometers.

Spring staging and autumn swarming.—A bat trap was used to capture bats in spring and autumn. Bats were trapped from dusk until 0000 – 0200 h at Buddy Penley Cave 17 - 20 April 2000. Trapping in autumn was on 8, 11, and 26 September and 11 October 2001 at the Bane entrance of Newberry-Bane Cave, and ran from dusk to 0100 h on 8 September and until 2300 h on the other nights.

Bats were identified to species and sexed. When time allowed, weight, right forearm length, time of capture, and reproductive status were recorded. During autumn, the rate of capture was so great that about 150 – 200 bats were released without data collection on 8 September, and about 50 bats were released on 11 September. Using

Chi-Square analysis, percentages of each species in the winter survey (expected ratio) were compared to percentages of each caught in autumn (observed ratio) for species where the catch was sufficient to test.

Summer cave use.—To determine summer use by a maternity colony or aggregation of male bats, most notably *C. t. virginianus*, autumn and winter intra-cave surveys included searches for accumulations of guano. In late May 2000, caves were searched for concentrations of bats, including the Attic of Buddy Penley Cave where a moderate accumulation of guano was noted during winter surveys.

RESULTS

Wintering bats.—During autumn trips in four caves, >7,000 bats of four species were found (Table 2). Most were *M. lucifugus*, and most were in Newberry-Bane (5 species) and Buddy Penley (4 species) caves. Only *M. lucifugus* and *Pipistrellus subflavus* (eastern pipistrelle) were found in Paul Penley and Coon caves. During winter, 12 caves were searched and 16,185 bats counted (Table 2); 89% (n = 14,479) were *M. lucifugus*. Newberry-Bane (6 species) and Buddy Penley (3 species) caves again contained the greatest number of bats. More bats were in Newberry-Bane (48% more than in autumn), Buddy Penley (197%), Paul Penley (107%) and Coon (285%) caves in winter than in autumn. About half the increase of bats in Newberry-Bane Cave and about a third of the increase in Buddy Penley Cave resulted from increases in areas surveyed in those caves. Paul Penley and Coon caves again had *M. lucifugus* and *P. subflavus*, and a single *Myotis septentrionalis* (northern myotis) was also found in Coon Cave. Munsey #1, Bane Spring, and Paul Penley caves had 100 - 1,000 bats. No bats were found in Munsey Twin #2. No endangered *C. t. virginianus* were found during autumn and winter cave surveys.

Myotis sodalis was found only in Newberry-Bane Cave, with the exception of a single individual in Buddy Penley Cave on 23 November (Table 2). On 22 November, 26% of the population was in Lower Junction with 74% in Upper Junction. The temperature in both areas was ≥8.5°C. During winter, bats had changed location, abandoning Lower Junction entirely, and Upper Junction in large part, although temperatures in both areas had dropped (Table 3). Instead, 88% of the population was in a new area, the Bane Entrance Passage, at a temperature that was lower than either of the other two areas (Table 3).

Like *M. sodalis*, *Myotis leibii* (small-footed myotis) was found only in Newberry-Bane Cave (Table 2). In autumn, one individual was found in the Junction area (9°C), and in winter, seven *M. leibii* were found hibernating between the Bane Entrance Passage and the Junction area (5.7 – 6.8°C). No *M. septentrionalis* were found during the autumn survey, but 12 were found in winter, 9 in Newberry-Bane Cave, scattered throughout the survey area, most near 9°C. Autumn surveys located 9 *Eptesicus fuscus* (big brown bat) and winter surveys located 15 hibernating at a wide range of temperatures (1.2° - 13.3°C).

The largest concentrations of *M. lucifugus* were found in Newberry-Bane and Buddy Penley caves during both autumn and winter (Table 2). Numbers of *M. lucifugus* in Newberry-Bane Cave increased by 45% (n = 1,725) between November and February, but bats were less concentrated in the North Subway. There were three times more bats in Buddy Penley Cave in winter than in autumn (Table 2), but about one-third were from an area not visited in autumn. Nevertheless, the number of bats

TABLE 2. Bats found during autumn 1999 and winter 2000 visits to caves in the Skydusky Hollow Cave System and nearby caves in the same karst system in Bland County, Virginia. Four caves were surveyed in autumn and 12 caves in winter; "*n*" refers to sample size.

Cave	*M. sodalist*		*M. lucifugus*		*M. septentrionalis*		*M. leibii*		*P. subflavus*		*E. fuscus*		
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	Total
22 - 24 November 1999													
Newberry-Bane	170	4.2	3,809	94.9			1	0.0	31	0.8	4	0.1	4,015
Buddy Penley	1	0.0	2,068	95.1					101	4.6	5	0.2	2,175
Paul Penley			370	85.8					61	14.2			431
Coon			312	54.1					265	45.9			577
Autumn Total	171	2.4	6,559	91.1			1	0.0	458	6.4	9	0.1	7,198
Mid-January - 5 March 2000													
Newberry-Bane	235	4.0	5,534	93.4	9	0.2	7	0.1	137	2.3	2	0.0	5,924
Buddy Penley			6,304	97.5	1	0.0			160	2.5			6,465
Paul Penley			833	93.5					58	6.5			891
Coon			1,296	58.4	1	0.0			920	41.5	2	0.1	2,219
Spring Hollow			21	84.0	1	4.0			3	12.0			25
Bane Spring			442	90.8					45	9.2			487
Munsey #1			44	36.1					78	63.9			122
Munsey #2									1	10.0	9	90.0	10
Munsey Twin #1									16	100.0			16
Munsey Twin #2													
Morehead's Pit			1	5.6					17	94.4			18
Springhouse									6	75.0	2	25.0	8
Winter Total	235	1.5	14,475	89.4	12	0.1	7	0.0	1,441	8.9	15	0.1	16,185

at Pit 1, the area of greatest concentration in both seasons, more than doubled (Table 3). Numbers of *M. lucifugus* in Paul Penley doubled between autumn and winter, and the number in Coon Cave increased by four times (Table 2); in both caves, locations used by the largest concentrations of bats changed between seasons (Table 3).

Although individual *M. lucifugus* were found across the range of temperatures available (1 – 14°C), concentrations in autumn were found at higher temperatures than were concentrations in winter (Table 3). In autumn, the largest concentrations were in Newberry-Bane Cave in North Subway (58% of the autumn total) at 9 - 9.5°C, and Pit 1 of Buddy Penley Cave (32%) at 7.9°C (Table 3). In winter, *M. lucifugus* were concentrated at Pit 1 (30% of the winter total) at 6.3 - 6.5°C and Guano Climb (10%) at 6.9°C in Buddy Penley Cave, in North Subway (20%) at 8.2 - 8.9°C and a portion of the Junction area (12%) at 7.4°C of Newberry-Bane Cave, and in Big Room of Coon Cave (9%) at 8.6 - 9.7°C (Table 3).

Pipistrellus subflavus used the most caves, 4 of 4 caves in autumn and 11 of 12 caves in winter (Table 2). Coon Cave contained over half the total in both autumn and winter, but Buddy Penley held 22% of autumn and 11% of winter populations. Temperatures were warmer in both caves in autumn than in winter (Table 3). In winter, *P. subflavus* concentrated in Main Passage (31% of the winter total) at 7.4 – 8.2°C and Big Room (33%); at 8.6 – 9.7°C of Coon Cave, and in Buddy Penley Cave at 6.5 – 7.4°C (Table 3). During winter, small concentrations of *P. subflavus* in Munsey #1, Paul Penley, and Bane Spring caves were generally in areas >8.0°C (Table 3).

Spring staging and autumn swarming.—Trapping at the entrance to Buddy Penley Cave for 4 nights in April 2000 produced 101 bats of four species: 63 *M. lucifugus*, 31 *M. septentrionalis*, 6 *P. subflavus*, and 1 *E. fuscus*. Female *M. lucifugus* were six times more common than males, but there were nearly equal numbers of male and female *M. septentrionalis*.

During autumn 2001, trapping on 4 nights at Newberry-Bane Cave, 885 bats of six species were processed: 27 *M. sodalis*, 603 *M. lucifugus*, 185 *M. septentrionalis*, 6 *M. leibii*, 60 *P. subflavus*, and 4 *E. fuscus*. Proportions of *M. sodalis*, *M. lucifugus*, and *P. subflavus* in the catch in autumn 2001 were different than proportions observed in Newberry-Bane Cave during winter 2000 (X^2 = 123.9; at $P<0.001$; df = 2). *Myotis lucifugus* was over represented in the winter survey and *P. subflavus* in the autumn survey. *Myotis sodalis* was similarly represented in samples from both seasons. In addition, *M. septentrionalis* was nearly absent from the winter survey (0.2%), excluding it from the analysis, but it was common in autumn (20.9%).

Catch of female *M. sodalis*, although small, was greater in mid-September than early September and early October, whereas captures of males, relative to females, increased through the samples (Figure 1a). Captures of female *M. lucifugus* remained relatively constant, but captures of males, relative to females, dropped dramatically over the autumn season (Figure 1b). More male than female *M. septentrionalis* were caught early and late in the sample season and the absolute catch appeared to increase late in the season (Figure 1c). The pattern for *P. subflavus* was similar to that of *M. lucifugus* (Figure 1d). *Myotis leibii* were caught on 8 September (2 male and 2 female), 26 September (1 male), and 11 October (1 male). On 26 September, one male *E. fuscus* was caught and on 11 October two males and one female were caught.

Summer maternity colonies.—No large accumulation of guano that would indicate summer use was found during autumn and winter intra-cave surveys. There was a

TABLE 3. Temperatures at which concentrations of three species of bats were found during autumn 1999 and winter 2000 surveys in caves of the Skydusky Hollow Cave System, Bland County, Virginia. Because not all bats were in areas of concentration, totals in this table do not necessarily match totals in Table 2.

Species Survey	Date	Cave	Location	Bats	Temp (^{o}C)
M. sodalis					
Autumn	22 Nov	Newberry-Bane	Lower Jct.	44	8.5
			Upper Jct.	126	8.9
Winter	5 Feb	Newberry-Bane	Lower Jct	0	7.2
			Upper Jct	29	8.7
			Bane Ent. Passage	206	7.0
M. lucifugus					
Autumn	22 Nov	Newberry-Bane	N. Subway	3,778	9.0 - 9.5
	23 Nov	Buddy Penley	Pit 1	2,068	7.9
	23 Nov	Paul Penley	Big Room	245	11.0
			Whisper Hall	67	10.0
	24 Nov	Coon	Main Passage	67	11.0
			Big Room	245	11.0
Winter	17 Jan	Coon	Main Passage	28	9.1
			Big Room	1,268	8.6 - 9.7
	19 Jan	Bane Spring	Front	383	7.4-8.3
			Pit	59	9.8
	3 Feb	Newberry-Bane	N. Subway	2,891	8.2-8.9
	5 Feb		Junction area	1,802	7.4
			Junction area	255	8.7
	4 Mar	Buddy Penley	Pit 1	4,280	6.3-6.5
			Pit	375	7.4
			Guano Climb	1,400	6.9
			Attic	210	8.4
	5 Mar	Paul Penley	Big Room	76	9.8
			Whisper Hall	755	9.4 - 9.8
P. subflavus					
Autumn	22 Nov	Newberry-Bane	all	31	9.0 - 11.0
	23 Nov	Buddy Penley	Entrance Passage	101	9.0
		Paul Penley	Whisper Hall	32	10.0
	24 Nov	Coon	Main Passage	175	11.0
			Big Room	90	11.0
Winter	17 Jan	Coon	Main Passage	451	7.4-8.2
			Big Room	469	8.6 - 9.7
	19 Jan	Bane Spring	Front	41	7.4 - 8.3
	28 Jan	Munsey #1	all	78	7.7 - 8.4
	3 - 4 Feb	Newberry-Bane	various	105	8.1 - 9.3
	5 Feb		Junction area	29	7.4
	4 Mar	Buddy Penley	all	160	6.5 - 7.4
	5 Mar	Paul Penley	Whisper Hall	47	9.4 - 10.2

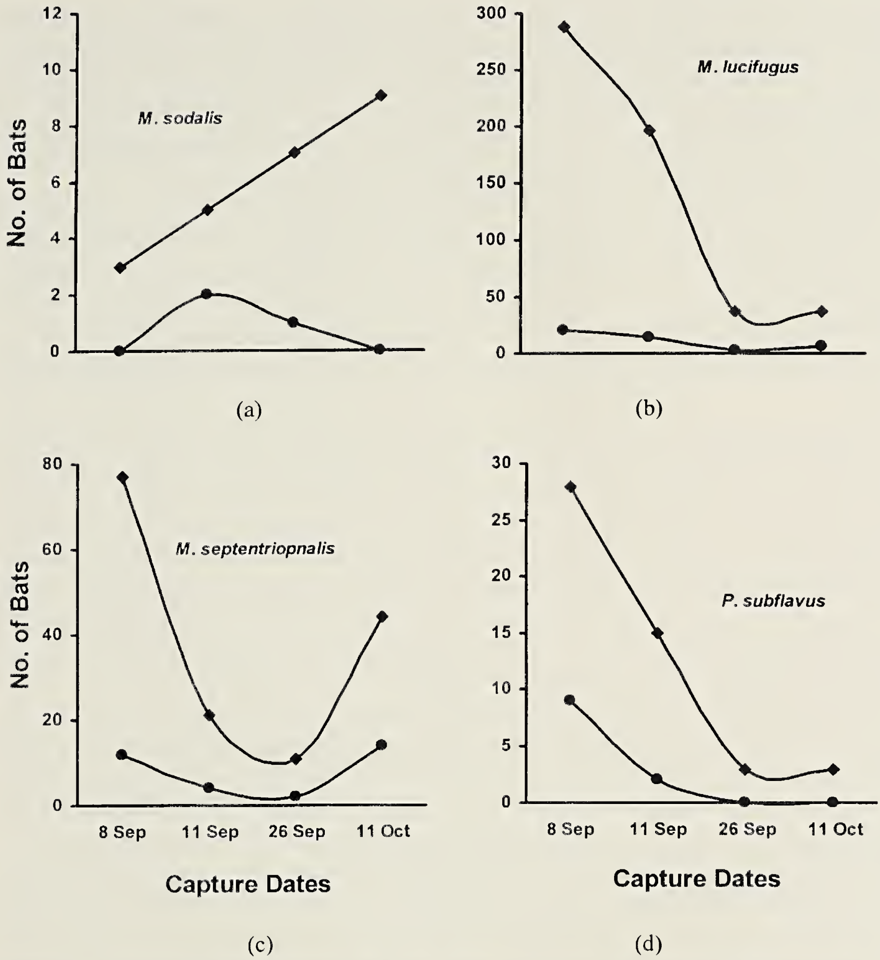

FIGURE 1. Captures of male (diamond) and female (closed circle) *M. sodalis* (a), *M. lucifugus* (b), *M. septentrionalis* (c), and *P. subflavus* (d) during autumn 2001 swarming. Note that numbers of bats are not to the same scale.

moderate accumulation of guano in the Attic of Buddy Penley Cave. When visited on 31 May 2000, no bats were present and there was no new accumulation of guano. The temperature was about 10°C.

DISCUSSION

Spring staging and autumn swarming.—Proportions of species of bats captured in spring and autumn varied among populations hibernating in the same caves. The greatest disparity was seen with *M. septentrionalis*, a species often caught at entrances to hibernacula in spring and autumn (Whitaker and Rissler 1992) but infrequently found during winter (Brack et al. 2003b, 2004).

The change in capture of bats as autumn progressed indicated a social component in use of the cave. Although there were disproportionately large numbers of males of all species, *M. sodalis* had the most dramatic shift in relative abundance of sexes during

autumn. Male *M. sodalis* are more common during swarming than females because they congregate near hibernacula to mate with females that are arriving for hibernation; females terminate autumn activities and enter hibernation before males (Cope and Humphrey 1977; LaVal and LaVal 1980). Richter et al. (1993) found that small male *M. sodalis* with insufficient fat reserves to survive the winter may remain active in hibernacula, possibly seeking an opportunity to copulate before dying.

Male *M. lucifugus* were much more abundant than females early in autumn, but numbers dropped precipitously over time, similar to patterns observed for this species at caves in Indiana (Humphrey and Cope 1976). Activity of *P. subflavus* declined earlier in autumn than for other species, perhaps signaling an earlier entry into hibernation. By contrast, activity of *M. septentrionalis* seemed to rebound late in autumn, and perhaps is related to greater activity during winter (Whitaker and Rissler 1992).

Winter hibernation.—Cave morphology strongly affects suitability for hibernation (Humphrey 1978) by affecting airflow and thus temperatures. Large complex systems offer more opportunities for the combination of characteristics needed to support hibernating bats. The Skydusky Hollow Cave System and its individual caves are complex and extensive (Zokaites 1995). Most species of bats make relatively characteristic and recognizable use of hibernacula, including temperature regimes and spatial associations (Brack et al. 2003b). In the caves of Skydusky Hollow, the locations within caves used by concentrations of bats often changed between seasons, similar to studies in Missouri (Myers 1964; Clawson et al. 1980)

Hibernating *M. sodalis* often form dense clusters in cool areas of hibernacula. *Myotis sodalis* did not use the traditional roost in the Bane Entrance Passage in autumn, but by winter had moved there, at 7°C, from the Upper and Lower Junction areas. About 12% of the population remained in Upper Junction at 8.7°C. These temperatures are not as cold as is often considered optimal for the species during mid-winter, i.e., 4 - 8°C, or perhaps more narrowly 3 - 6°C (USFWS 1999). Further, cooler temperatures (6.3 – 6.5°C) were available at the bottom of Pit 1 in Buddy Penley Cave. Hall (1962) in the Midwest, Henshaw and Folk (1966) in Kentucky, and Humphrey (1978) in midwestern and eastern states, considered mid-winter temperatures used by *M. sodalis* to be 4 - 5°C, 2 - 3°C, and 4 - 8°C, respectively, but they did not provided supporting documentation. In contrast, Brack et al. (2003b) completed 25 years of studies in many of the caves addressed by Hall (1962) and Humphrey (1978) in Indiana, and they documented increasing populations of *M. sodalis* in these caves, hibernating in areas with mean mid-winter temperatures of 6 - 8°C. In Missouri, Myers (1964) found *M. sodalis* hibernating at 4.4 - 16.7°C, but considered 7.8°C representative; mid-winter temperatures at clusters in three caves were 5.0 - 9.2°C ($n = 6$; $\bar{X} = 7.1$; $SD = 1.4$). Also in Missouri, Clawson et al. (1980) found *M. sodalis* hibernating at 6 - 8°C in late January. Thus, temperatures used by *M. sodalis* in Skydusky caves were similar to those reported in other studies.

Myotis lucifugus uses many caves (Dalton 1987; Brack et al. 2003b) and small numbers often hibernate in warm areas, sometimes giving the impression that this species prefers the warmer temperatures that are available in caves for hibernation (Brack et al. 2003b, 2004). In Skydusky caves, the largest concentration of *M. lucifugus* ($n = 4{,}280$) hibernated at 6.5°C, at the bottom of Pit 1 in Buddy Penley in an area cooler than areas used by *M. sodalis*. The remaining 6,300 *M. lucifugus* hibernated at

temperatures similar to, or slightly less than, temperatures used by *M. sodalis*. In a limestone mine in Ohio, *M. lucifugus* similarly used cooler areas, which were also less thermally stable, than did *M. sodalis* (Brack unpublished data).

Pipistrellus subflavus is found hibernating in more caves than other species of bats, and it typically hibernates singly and dispersed at warm, stable temperatures (Hassell 1967; Brack et al. 2003b, 2004). As in other caves, *P. subflavus* hung singly or occasionally in pairs and used a stable, warm area, but the number of *P. subflavus* in Coon Cave was much greater than observed in most caves. The species arouses less frequently than other species (Brack and Twenty 1985; Twenty et al. 1985), which may offset the cost of hibernating at warmer temperatures. This species often collects beads of moisture on guard hairs, which increases the mass of individuals and it is an interesting question whether this water, suspended between the bat and its environment, may act as a heat sink, dampening fluctuations in air temperature.

Little is known about *M. septentrionalis* and *M. leibii* during the season of hibernation. *Myotis septentrionalis* is readily caught at cave entrances in spring and autumn, providing indirect evidence of winter use (Whitaker and Rissler 1992), but is infrequently found in hibernation (Brack et al. 2003b). When found in winter, it is often deep in cracks or tight crevices in warm stable areas of the cave. *Myotis leibii* is believed to hibernate at cold temperatures (Best and Jennings 1997), an inference based on limited observation.

Eptesicus fuscus, a common summer resident in western Virginia, was uncommon in these caves in winter. In natural hibernacula, it is considered a hearty species that hibernates near entrances where temperatures may get very cold (Brack and Twente 1985), and it moves among hibernacula during winter. However, *E. fuscus* commonly hibernates in walls of old brick houses (Whitaker and Gummer 1992), where temperatures are 3 - 20°C ($\bar{X}$= 10°C).

Intra-cave movements of bats during the season of hibernation are poorly documented. Like Skydusky caves, Clawson et al. (1980) documented an increasing concentration of *M. sodalis* in areas considered traditional hibernacula roosts between autumn and mid-winter. Similar to Skydusky, Hassell (1967) found that *M. sodalis* hibernated in areas that got colder through the first half of the winter and warmer during the latter half of winter.

Because *M. sodalis* is listed as endangered, the occurrence of even a single individual has sometimes been used to identify a cave or mine as a hibernaculum. A single *M. sodalis* was found in Buddy Penley Cave in autumn; none were present in winter. There are several similar occurrences in Indiana: (1) an individual *M. sodalis* was in a cave one winter, and none were present the next (Brack et al. 2004), and (2) an *M. sodalis* was netted at a cave entrance in autumn, but no *M. sodalis* have been found during several winter surveys over a 25-year period (Brack et al. 2003b). In Ohio, a single *M. sodalis* was caught at a mine portal, but four additional nights of sampling during two seasons did not produce additional *M. sodalis* (Brack, unpublished data). These occurrences indicate that *M. sodalis*, and likely other species, visits caves and mines that are not used as hibernacula. Bats undoubtedly explore caves or parts of caves not suitable for hibernation, especially during the spring and autumn migration and transient periods.

Although Hassell (1967) reported that *M. lucifugus* occupied the same locations within caves throughout winter, we found that numbers and proportions of *M. lucifugus*

in specific regions of Newberry-Bane, Paul Penley, and Coon caves changed dramatically over the season of hibernation. It is probable there were also inter-cave movements; Whitaker and Rissler (1992) documented bats exiting and entering hibernacula throughout winter. The net result of these population shifts was to concentrate hibernating *M. lucifugus* in cooler areas of the cave. Similarly, there were large changes between autumn and winter in numbers and proportions of *P. subflavus* in parts of Coon Cave. It is probable that in addition to temperature, the social nature of bats affects the locations they used for hibernation. Raesly and Gates (1987) found that the presence of other bats, of all species, strongly influenced use of sites for hibernation.

Summer maternity colonies.—No concentrations of bats were found in Skydusky caves during summer. The most likely candidate for summer use was *C. t. virginianus*, although there are records of bachelor colonies of *M. grisescens* in Lee County Virginia (Webster et al. 1985). There was no large accumulation of guano indicative of past use, and there were no bats in the Attic of Buddy Penley Cave in late May. The Attic was cooler (10°C) than maternity roosts used by *C. t. virginianus* in Kentucky (Lackie et al. 1994) and the closely related subspecies *C. t. ingens* (Ozark big-eared bat) in Oklahoma (Clark et al. 1996) at this time of year (12.8 - 16.3°C).

Summary.—The caves of Skydusky Hollow held >16,000 bats of 6 species in winter 2000, which is an important resource for the Commonwealth of Virginia and the region. Most (89%) were *M. lucifugus*, although 9% were *P. subflavus* and 1% the federally endangered *M. sodalis*. No endangered *C. t. virginianus* were found. Most bats were in two caves, Newberry-Bane (37%) and Buddy Penley (40%), including endangered *M. sodalis*, although there was an unusually large concentration of *P. subflavus* (64% of this species and 6% of the total) in Coon Cave. Of the three most common species, the largest mid-winter concentration of *M. lucifugus* was at the coldest temperature (6.3-6.5°C), *M. sodalis* at a more moderate temperature (7.0°C), and *P. subflavus* at the warmest temperature (8.6-9.7°C). No concentration of bats used the caves during summer. Proportions of species captured in spring and autumn were not consistent with wintering populations, with the greatest disparity shown by *M. septentrionalis*, a species often caught at hibernacula in spring and autumn but infrequently found in winter. Changes in proportions of males and females caught over autumn indicate a social function to autumn swarming.

ACKNOWLEDGMENTS

All authors contributed to field and reporting efforts. American Electric Power (AEP) and Virginia Department of Game and Inland Fisheries funded portions of these studies. Ron Poff (AEP) played a vital role in assuring completion of the studies. We thank landowners who allowed access to caves: Molly and Jerry Thompson, Robert Banes, Gene Harman, Billy Dilman, Joe Bane, Ellis Morehead, Bob Munsey. Many individuals participated in caving trips, and, without them, the surveys would not have been as safe or as successful: Bobby Zokaites, Joe Thompson, Steve Wells, Steve LePera, Brad Atkinson, Eileen O'Malley, Matt Burnett, Kirk Digby, Raymond Sira, Don Anderson, Walter Pirie, Michael Malsburn, Charlie Jones, and Terri Brown. The 1992 bat count was led by Ed Devine in Paul Penley, Jerry Redder in Buddy Penley, Barbara Graham in Bane Spring, Paul Kirchman in Spring Hollow, and Joe and Carol Zokaites and Jean Simonds in Newberry Bane. We thank Dean Metter and Gary Finni for inspiration.

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JEFFRESS RESEARCH GRANT AWARDS

The Allocations Committee of the Thomas F. and Kate Miller Jeffress Memorial Trust has announced the award of Jeffress Research Grants to the institutions listed below to support the research of the investigator whose name is given. The Jeffress Trust, established in 1981 under the will of Robert M. Jeffress, a business executive and philanthropist of Richmond, supports research in chemical, medical and other natural sciences through grants to non-profit research and educational institutions in the Commonwealth of Virginia. The Jeffress Research Grants being announced here have been awarded in 2003.

The Jeffress Memorial Trust is administered by Bank of America. Additional information about the program of the Trust may be obtained by writing to: Richard B. Brandt, Ph.D., Advisor, Thomas F. and Kate Miller Jeffress Memorial Trust, Bank of America, Private Bank, P. 0. Box 26688, Richmond, VA 23261-6688. An unofficial website is listed under Grants and Awards, www.vacadsci.org.

William P. Anderson, Radford University. Collection of Water Level Data to Test New Methods for Estimating Recharge in Water-Table Aquifers. $10,000. (one year renewal).

Todd D. Averett, The College of William and Mary. Neutron Spin Structure Studies Using High Density Polarized ^{3}He Targets. $10,000. (one year renewal).

Stephen F. Baron, Bridgewater College. Regulation of Excellular Polyhydroxalkanoate Depolymerase Synthesis in Streptomyces spp.5A. $27,320. (one year).

Deborah C. Bebout, The College of William and Mary. Investigation of Silica Supported Copper Complexes as Biometrics of Micronuclear Monooxygenases. $10,000. (one year renewal).

John J. Beck, Sweet Briar College. Structure-Activity Relationships of Aromatic Analogs of (Z)-Ligustilide: A Natural Product from *Ligusticum* Species. $10,000. (one year renewal).

Matthew J. Beckman, Virginia Commonwealth University/Medical College of Virginia. Arthritis and the Importance of Ets-2 in Urokinase-Plasminogen Activator Expression. $10,000. (one year renewal).

Wade E. Bell, Virginia Military Institute. The Role of Calcium in Paramecium Chemoresponse: Elucidation of Mechanisms for Calcium Influx. $10,000. (one year renewal).

Mark P. Birkenbach, Eastern Virginia Medical School. Characterization of Interleukin-27 Function in Immune Response to Murine Cytomegalovirus (MCMV). $20,000. (one year).

Robert A. Bloodgood, University of Virginia School of Medicine. Calcium Regulation of Whole Cell Locomotion. $10,000. (one year renewal).

Timothy Bos, Eastern Virginia Medical School. Regulation of Breast Cancer Gene Targets by the AP-1 Transcription Factor. $10,000. (one year renewal).

Karen J. Brewer, Virginia Polytechnic Institute and State University. Binding Metal Centers to Photochemically Active Metal Sites. $10,000. (one year renewal).

Stephen G. Cessna, Eastern Mennonite University. Reactive Oxygen Production During Salinity Tolerance Responses in Tobacco Cells: Relationship to Cytosolic $Ca^{2\sim}$ Fluxes. $10,000. (one year renewal).

Jennifer A. Clevinger, James Madison University. Phylogenetic Analysis of [Silphium} and [Berandiera] (Asteraceae) Using DNA Sequence data. $10,000. (one year renewal).

Stuart C. Clough, University of Richmond. The Preparation and Application of 5-chioro-5-ary!-2, 4-pentadienoates to the Regioselective Synthesis of Heterocycles and Carbocycles. $20,000. (one year).

Gary G. Coté, Radford University. Regulation of Plant Crystal-Containing Idioblast Cells by Herbivory. $8,820. (one year renewal)

Brian Cusato, Sweet Briar College. The Pavlovian Conditioning on Sexual Behavior and Fertility in Female Japanese Quail *(Coiurnixjaponica).* $25,000. (one year).

Antonio del Castillo, Virginia Commonwealth University/Medical College of Virginia. Role of Feto Protein Transcription Factor (FTF) in Bile Acid Synthesis. $25,000. (one year).

Christopher Del Negro, The College of William and Mary. Do Pacemaker Neurons Generate the Rhythum for Breathing?. $30,000. (one year).

Michael R. Deschenes, The College of William and Mary. Effects of Senescence on Neuromuscular Adaptations to Disease. $30,000. (one year).

Anca D. Dobrian, Eastern Virginia Medical School. Vascular Reactivity and Oxidative Balance in Large and Small Arteries in a Rat Model of Obesity-Induced Hypertension. $10,000. (one year renewal).

James Eason, Washington and Lee University. The Mechanisms of Defibrillation During Acute Myocardial Ischema $16,000. (one year).

Sergei A. Egorov, University of Virginia. Interactions Between Nanoparticles in Supercritical Fluids. $10,000. (one year renewal).

Joseph J. Feher, Virginia Commonwealth University/Medical College of Virginia. Continuous Measurement of Superoxide During Ischemia-Reperfusion Injury of Intact Rat Hearts. $28,863. (one year).

Marcia B. France, Washington and Lee University. Chiral Schiff Base Complexes as Catalysts for Assemetric Cyclopropanation. $10,000. (one year renewal).

Babette Fuss, Virginia Commonwealth University/Medical College of Virginia. Novel Mechanisms in CNS Mylelination: Role of PD-1aIATX. $10,000. (one year renewal).

Ning Gao, Virginia Commonwealth University/Medical College of Virginia. Molecular Mechanisms of the Anticarcinogenic Effects of Indole-3-Carbinol. $25,000. (one year).

George W. Gilchrist, The College of William and Mary. The Genetic Architecture of Rapidly Evolving Traits in Invading Populations of *Drosophila subobscura.* $10,000. (one year renewal).

Glenda Gillaspy, Virginia Polytechnic Institute and State University. Inositol Synthesis and Catabolism in Plants. $15,000. (one year).

Emma Goldman, University of Richmond. Synthesis and Characterization of a Series of Dicopper Compounds for Use as Electro catalysts in the Reduction of Carbon Dioxide. $16,450. (one year).

Douglas S. Graber-Neufeld, Eastern Mennonite University. Renal Transport of Organic Anions in Insects: A Role for Handling Environmental Toxins. $10,000. (one year renewal).

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